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New *Scutellastra* (Gastropoda: Patellidae) species from the lower Miocene Navidad Formation of central Chile and the lower-middle Miocene Cantaure Formation of Venezuela

Sven N. Nielsen

Universidad Austral de Chile
Instituto de Ciencias Ambientales y Evolutivas
Casilla 567, Valdivia, Chile
sven.nielsen@uach.cl

Bernard Landau

Naturalis Biodiversity Center
Leiden, The Netherlands
and
Centro de Geologia da Universidade de Lisboa
Lisboa, Portugal
and
International Health Centres
Av. Infante de Henrique 7
Areias São João, P-8200-261
Albufeira, Portugal
bernielandau@sapo.pt

ABSTRACT

New species of the patellid gastropod genus *Scutellastra* are described from the lower Miocene Navidad Formation of central Chile and the lower-middle Miocene Cantaure Formation of Venezuela. *Scutellastra arayae* new species is the first fossil record of a patellid from Chile and *S. venezuelana* new species is the first from tropical America. This genus is today restricted to southern Africa and the western Pacific, with the exception of *S. mexicana* from Central America. Together with contemporaneous fossil occurrences in New Zealand, these new records show that *Scutellastra* had a much wider distribution when water temperatures were higher during the mid-Cenozoic.

Additional Keywords: Paleontology, marine, Patellogastropoda

INTRODUCTION

The systematic position of the genus *Scutellastra* H. and A. Adams, 1854 was considered problematic in the Southern Synthesis (Lindberg, 1998), whereas it is clearly included in Patellidae in the phylogenetic analysis of Ridgway et al. (1998). Further investigations by Koufopanou et al. (1999), Lindberg (2007), and Nakano and Ozawa (2007) suggested that the genus *Scutellastra* may be polyphyletic with respect to the genera *Helcion* Montfort, 1810 and *Cymbula* H. and A. Adams, 1854. Lindberg (2007) also mentioned a “scutellastrid clade” being the “sister taxon of [...] the Patellidae” but did not formally name it. It would contain the genera *Scutellastra*, *Helcion*, and *Cymbula*. We here follow the traditional view that recognizes the sole family Patellidae within Patelloidea (Bouchet and Rocroi, 2005).

Extant species of *Scutellastra* are present almost exclusively in the Atlantic, in southern Africa, and in the Indian Ocean, in southern Australia (Ridgway et al., 1998), with few species extending throughout the western Pacific, and only *S. mexicana* (Broderip and Sowerby, 1829) is present in the eastern Pacific, in the Americas, ranging from western Mexico to Peru. Species of *Scutellastra* are usually intertidal, but some live just subtidally (Lindberg, 1998). They are generally found in tropical to subtropical regions, with the species of southern Australia being the temperate end-members. The fossil record of *Scutellastra* goes back to the upper Cretaceous of Japan (Kase and Shigeta, 1996).

Patellogastropod limpets are a dominant group today in intertidal environments of Pacific southern South America, represented by the nacellid genus *Nacella* (Valdovinos and R  th, 2005; Gonz  lez-Wever et al., 2011) and the lottiid genus *Scurria* (Espoz et al., 2004). The Chilean fossil record of limpets in beds older than Pleistocene is scarce. Only a single specimen of *Nacella* (*Patinigera*) *intiforma* DeVries, 2008 from the Huenteguapi Sandstone (Le Roux et al., 2008) on Arauco Peninsula and the holotype of *Nacella* (*Patinigera*) *nielsenii* DeVries, 2008 from Chilo   Island (Watters and Fleming, 1972) are known from the Neogene of Chile. The only other large patellogastropod limpet is the smooth-shelled nacellid *Cellana fuenzalidai* (Herm, 1969) from the Pliocene of northern Chile (Herm, 1969; Lindberg and Hickman, 1986). All these belong in the family Nacellidae.

The tropical American Neogene patellogastropod limpet record is even poorer, with no fossil species at all described from any of the rich Caribbean or Panamic Pacific assemblages, except for the shell illustrated by Lindberg (2007, text-figure 8B) as *Scutellastra* sp. from

the Pliocene of Venezuela. Lindberg (2007) did not provide the locality for this specimen, but, according to its locality record, it was collected at approximately 300 m south of Casa Cantaura (D.R. Lindberg personal communication), which is the only place where we have found representatives of *Scutellastra* in Venezuela. It is undoubtedly conspecific with the new Venezuelan species described herein and dates therefore from the Miocene, not Pliocene.

GEOLOGY OF FOSSIL-BEARING LOCALITIES

Chile: The Chilean *Scutellastra* comes from reddish sandstones of the Navidad Formation (Encinas et al., 2006) at Punta Perro, central Chile (Figure 1). These deposits were dated as upper Miocene by Finger et al. (2007, locality PPN) based on misidentified foraminifera (Finger, 2013). The mollusk assemblage was interpreted as being reworked from lower Miocene beds based on comparison with southern Peru (DeVries and Frassinetti, 2003; Finger et al., 2007), an interpretation confirmed with strontium isotope dating by Nielsen and Glodny (2009). Recently revised identification of stratigraphic index foraminifera (Finger, 2013), however, now agrees with a lower Miocene age for the Navidad Formation

and also explains earlier assignments to younger ages (e.g., Ibaraki, 1992). These new data provide a consensus for the lower Miocene age of the Navidad Formation. The displacement scenario of Finger et al. (2007) is still valid, although it has now been demonstrated that contemporaneous shallow-water deposits were transported into bathyal depths, as indicated by the strontium isotope data of Nielsen and Glodny (2009). Many shallow-water taxa occur in sediments intercalated with deep-water deposits containing a completely different fauna (see Finger et al., 2007).

The assemblage from the same concretionary block that contained the *Scutellastra* specimen includes *Pinna semicostata*, *Glycymeris* sp., *Astele chilensis*, *Echinophoria monilifer*, *Distorsio ringens*, *Glossaulax pachystoma*, *Magnatica subsolida*, *Sinum subglobosum*, *Lamprodomina dimidiata*, *Testallium cepa*, *Austrotoma echinulata*, *Inquisitor lingulacanthinus*, *Dentalium* sp. and represents the typical shallow-water Navidad assemblage (see Finger et al., 2007; Griffin and Nielsen, 2008; Kiel and Nielsen, 2010).

Venezuela: The Venezuelan *Scutellastra* material herein described and discussed comes from the San José de Cocodite region in the Paraguaná Peninsula of northern Venezuela (Falcon State). The collection site where

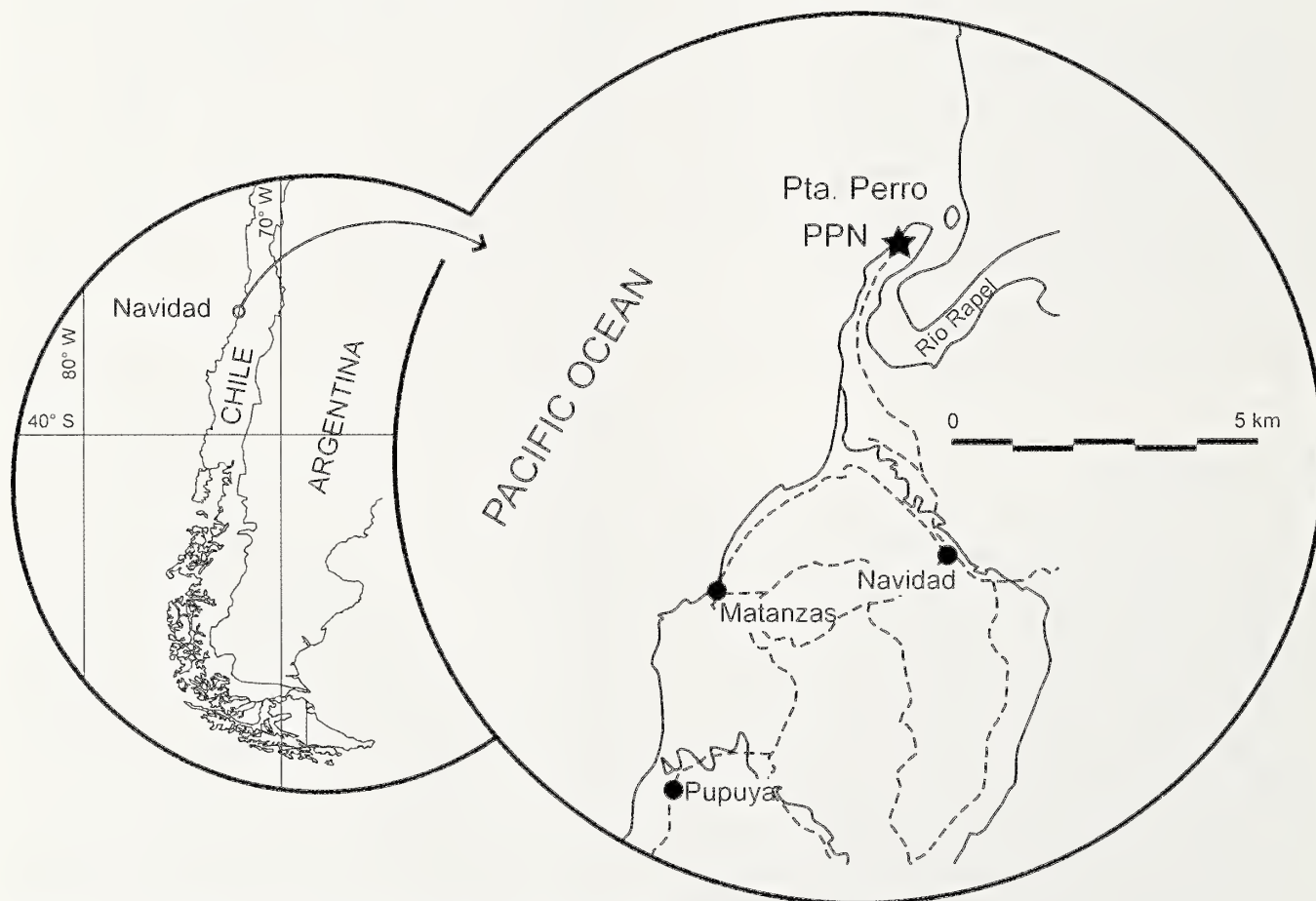


Figure 1. Geographic location of the study site in the Punta Perro region, in Chile.

it originates from is located in the Cantaure area, 3.4 km West of the church of the village of San José de Cocodite (as the crow flies), at an altitude of approximately 140 m above sea-level on a acacia and cactus covered area approximately 400 m south of Casa Cantaure with the approximate geographic coordinates: 11°56'24.1" N, 70° 01' 04.5" W (Figure 2; location of Casa Cantaure after Griffiths et al., 2013: 11°56'35.9" N, 70°01'10.8" W).

The specimens were collected from a thick, friable, yellow, fine sandstone bed containing an abundant and diversified molluscan assemblage (mostly gastropods and bivalves with rare nautiloid cephalopods), as well as other elements such as barnacles and corals. This bed is part of the Cantaure Formation (Jung, 1965; Hunter and Bartok, 1974), which, as a whole, according to Díaz de Gamero (1974), is correlated with the planktonic foraminiferal biozones *Globigerinatella insueta* and *Praeorbulina glomerosa* of Bolli (1966), biozones N7 and N8 of Blow (1969), which in turn, according to the latest geologic time scale of Gradstein et al. (2012), correspond to the Lower to Middle Miocene transition, upper Burdigalian to lower Langhian. Rey (1996) corroborates this biostratigraphic correlation stating that the Cantaure calcareous nannofossil assemblage contains the *Helicosphaera ampliapertura* and *Sphenolithus heteromorphus* markers corresponding

to the biozones NN4 and NN5 of Martini (1971), which broadly correlate with the above mentioned foraminiferal zones.

In several recent papers, however, the Cantaure Formation continues to be assigned to the Lower Miocene, Burdigalian, after the traditional correlation of Díaz de Gamero (1974) and Rey (1996). Aguilera and Rodríguez de Aguilera (1999), based on planktonic foraminifera data from a personal communication by Collins, place the Cantaure Formation in the Lower Miocene, Burdigalian. Griffiths et al. (2013), based on $^{87}\text{Sr}/^{86}\text{Sr}$ isotope data obtained from corals, assign an age of between 16.3 and 16.6 Ma to the fossils of Cantaure, placing them in the Burdigalian. These authors further comment that the isotopic results obtained are in good agreement with the traditional biostratigraphic age estimates for the Cantaure Formation based on the identification of the N7–N8 planktonic foraminiferal zones by Díaz de Gamero (1974) and the nannofossil biozones NN4–NN5 by Rey (1996). Anderson and Roopnarine (2005), on the other hand, in their Table 2, place the Cantaure Formation in the Burdigalian–Langhian, straddling the Lower–Middle Miocene boundary.

The Cantaure Formation consists of a sedimentary sequence approximately 75 m in thickness and mainly

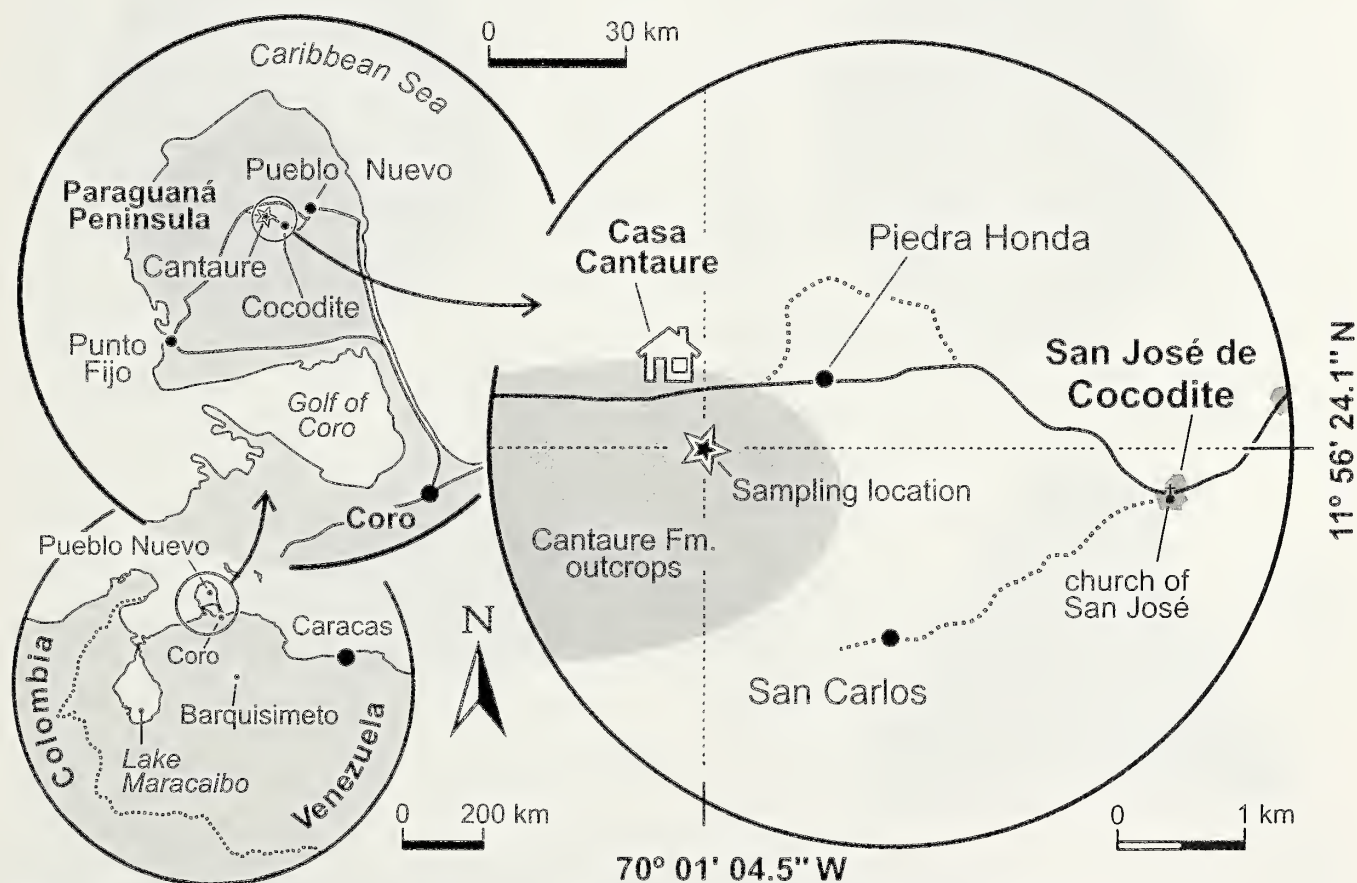


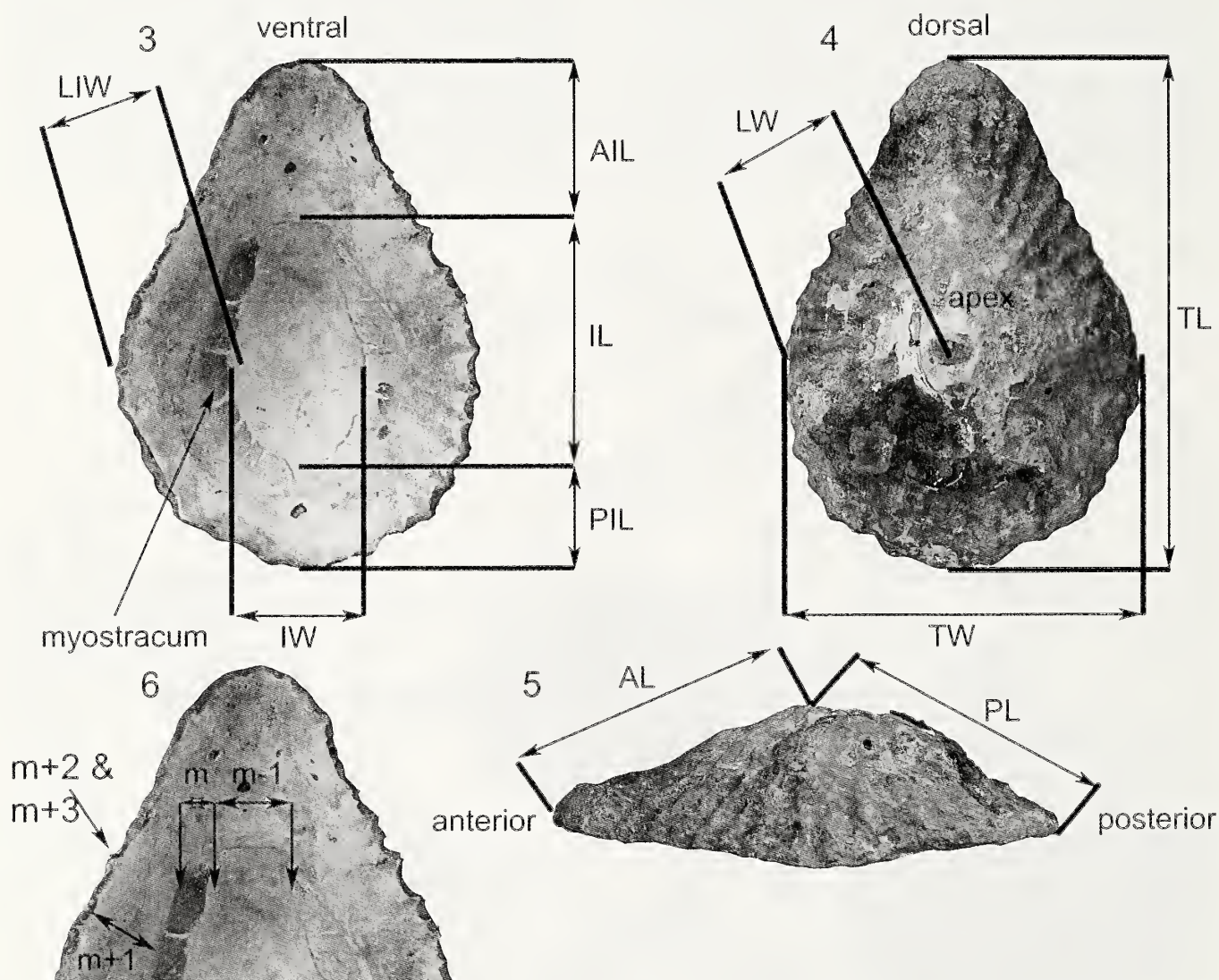
Figure 2. Geographic location of the study site in the Cantaure region, Paraguaná Peninsula, in Venezuela.

composed of fossiliferous silts, silty sandstones, and fine to medium sandstones interbedded with thin algal limestones (Hunter and Bartok 1974; L xico Estratigr fico de Venezuela, 1997; Aguilera et al., 2013). A diverse fossil assemblage, particularly rich in mollusks, but also featuring corals, decapods and cirripedian crustaceans, and fish remains, has been identified in the sediments of the Cantaure section, especially in its lower part (e.g. Jung 1965; Nolf and Aguilera 1998; Aguilera and Rodrigues de Aguilera, 1999; Griffiths et al., 2013). Locally, decimetric boulders of limestone with *in situ*-attached valves of the shallow marine bivalve *Spondylus* sp. may be observed within the friable fine sandstone beds. This fossil assemblage is indicative of a shallow to coastal tropical marine environment, with clear water and marine euhaline salinity (Jung, 1965; D az de Gamero, 1974; Nolf and Aguilera, 1998; Aguilera et al., 2013; Griffiths et al., 2013).

MATERIALS AND METHODS

The Chilean material described herein comes from the Covacevich and Frassinetti collection, housed in the Museo Nacional de Historia Natural, Santiago, Chile. The Venezuelan material described here is from the Gibson-Smith collection, housed in the Naturhistorisches Museum Basel (NMB), Switzerland, and the Bernard Landau collection, housed in the Naturhistorisches Museum Wien, Austria.

In the systematic descriptions of the new species, we have followed the morphometric model suggested by Jerardino and Navarro (2008) and MacClintock (1967) (Figures 3–6). Following the convention established by MacClintock (1967), the layers are numbered by reference to the myostracum (m); starting at the outside of the shell, they are designated m+3, m+2, m+1, m and



Figures 3–6. Morphometric measurements of patellogastropod limpet; *Scutellastra venezuelana* new species. Figures 3–5 adapted from Jerardino and Navarro (2008, p. 1025, fig. 1) TL = Total length; AL = anterior length; PL = posterior length; TW = total width; LW = lateral width; AIL = anterior inner length; IL = inner length; PIL = posterior inner length; IW = inner width; LIW = lateral inner width. Figure 6 adapted from MacClintock (1967) m = myostracum.

$m-1$. Although MacClintock (1967) distinguished $m+2$ and $m+3$ layers in the shells of patellids, Ridgeway et al. (1998) found that these were not clearly separable. In both new species the width of the $m+1$ layer is greater than half of the width of the combined outer ($m+1$, $m+2$, $m+3$) layers (see Figures 3, 5, 7, 10, 12). This character is seen in the genera *Scutellastra*, *Lottia*, and *Acmaea* (Ridgeway et al., 1998). The relatively large and solid shells with strong radial dorsal sculpture suggest placement in the genus *Scutellastra*.

Abbreviations: SGO.PI., Museo Nacional de Historia Natural, Santiago, Chile; NHMW, Naturhistorisches Museum Wien, Austria; NMB, Naturhistorisches Museum Basel, Switzerland.

SYSTEMATIC PALEONTOLOGY

Superfamily Patelloidea Rafinesque, 1815
Family Patellidae Rafinesque, 1815

Genus *Scutellastra* H. and A. Adams, 1854

Type Species: *Patella plicata* Born, 1778 (= *P. barbara* Linnaeus, 1758) by subsequent designation of Wenz (1938, see Ridgeway et al., 1998); Recent, South Africa.

Scutellastra arayae new species (Figures 7–9)

Description: Shell large, thick, oval, heavily ornamented with very coarse irregular radial ribs projecting notably at margin. Seven primary ribs, one secondary rib in each interspace, one tertiary rib between primaries and secondaries, additional lesser ribs in all interspaces and on major ribs. Apex situated anteriorly. Muscle scar horseshoe-shaped, open anteriorly. Venter with deep, U-shaped myostracum (m); $m-1$ about 1/3 total width of shell at level of opening of myostracum; $m+1$ wide, width about 4/5 in of $m-1$, $m+2$ and 3 narrow (numbering following MacClintock, 1967).

Type Material: Holotype SGO.PI.6650 from Punta Perro, height 55 mm, diameter 93 mm (incomplete) \times 92.6 mm, Covacevich and Frassinetti locality 241080.1. Concretionary block with small *Pinna semicostata*.

Type Locality: Punta Perro, lower Miocene Navidad Formation, central Chile.

Other Material Examined: Known only from holotype.

Distribution: Only known from the type locality.

Etymology: Named after Ivette Araya, paleontology collections manager at Museo Nacional de Historia Natural, Santiago.

Measurements: Measurements follow Jerardino and Navarro (2008). Total length (TL) > 93 mm; anterior length (AL) \sim 51.3 mm; posterior length (PL) unknown;

total width (TW) 92.6 mm; lateral width (LW) 50 mm; anterior inner length (AIL) 19 mm; inner length (IL) 60 mm; posterior inner length (PIL) unknown; inner width (IW) 36.2 mm; lateral inner width (LIW) > 26.2 mm.

Discussion: *Scutellastra arayae* new species has few coarse projecting ribs and can be easily distinguished from species with a smooth or crenulate margin, including *S. mexicana*. The apex of *S. arayae* lies anteriorly while that of *S. flexuosa* (Quoy and Gaimard, 1834) from Australia is nearly central. *Scutellastra chapmani* (Tenison-Woods, 1876) from Australia and *S. longicosta* (Lamarck, 1819) from South Africa have better defined and more projecting ribs. *Scutellastra barbara* (Linnaeus, 1758) and *S. exusta* (Reeve, 1854), both from South Africa have more and finer ribs.

According to Beu and Maxwell (1990) two fossil species of *Scutellastra* are known from New Zealand, the upper Oligocene–early Miocene *S. aurorae* Fleming, 1973 and the early Miocene *S. cooperi* (Powell, 1938), which would both be roughly contemporaneous with the Chilean species. Judging from the original figures, *S. aurorae* has a rather smooth margin and more and weaker ribs while *S. cooperi* has stronger projecting ribs than *S. arayae*.

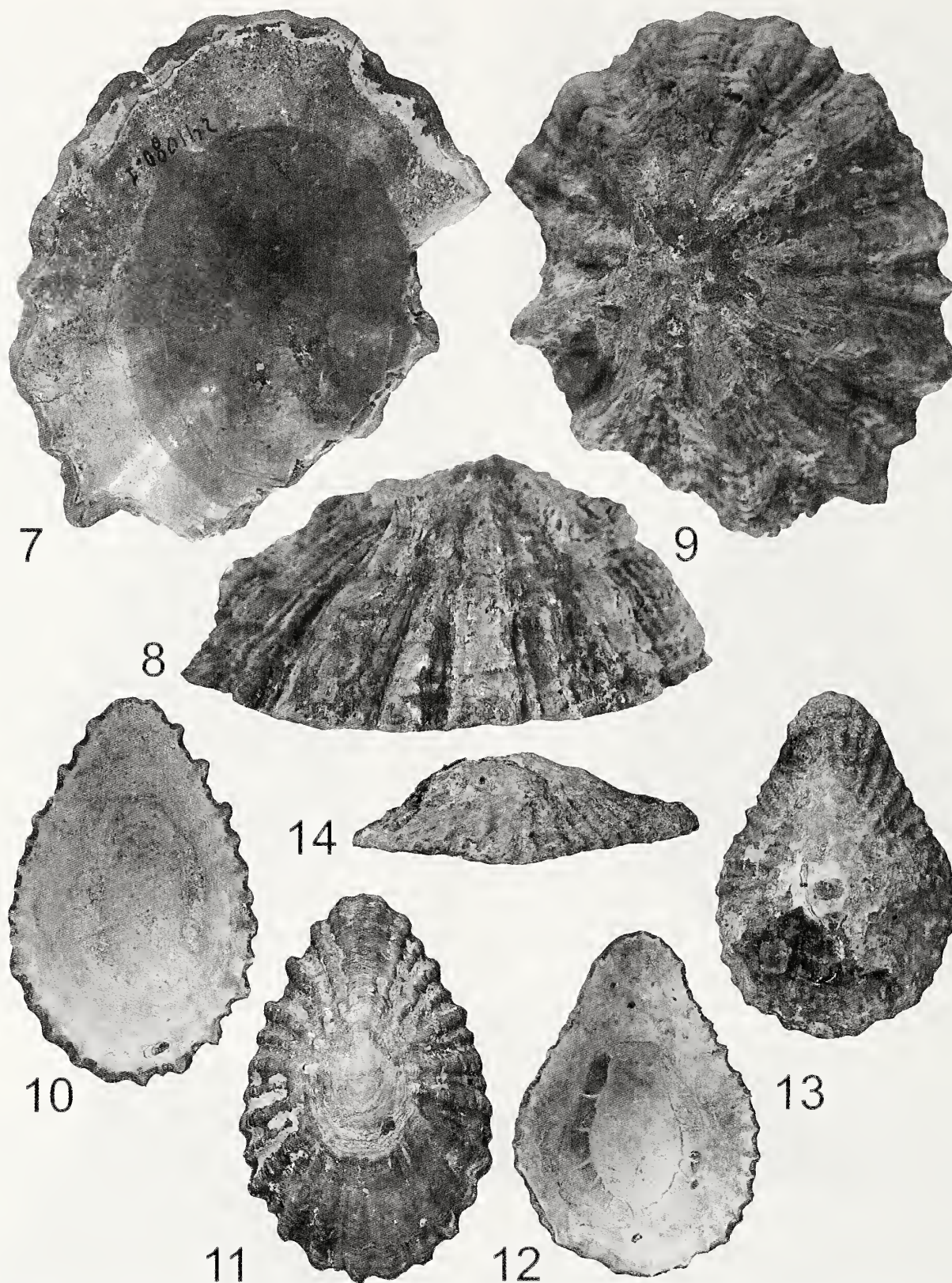
Several species of *Scutellastra* are known to be gardeners. Some species garden coralline algal substrate in their periphery, feeding either on those coralline algae or on other red algae growing on this substrate while other species maintain patches of algae on which they graze (Lindberg, 2007). Patch and periphery gardeners can be recognized morphologically since periphery gardeners exhibit an anteriorly extended shell while the shells of patch gardeners have a rounded anterior end. Both forms can thus be recognized in the fossil record and their ecology may be inferred as was done by Lindberg (2007) who figured the typically extended shell form of a fossil specimen from Venezuela that was reported as of Pliocene age but, as mentioned earlier, is the Miocene species described below. *Scutellastra arayae* does not show an anteriorly extended shell and is therefore considered to belong to the patch-gardening group.

Scutellastra venezuelana new species (Figures 10–14)

Scutellastra sp.—Lindberg, 2007, p. 230, fig. 8B.

Description: Shell moderately large, up to 90 mm in length, solid, depressed, pear-shaped, with anterior end produced, but not constricted at neck. Sculpture of coarse radial ribs on dorsum, most of which of primary strength and deeply corrugate the margin. Venter with deep, U-shaped myostracum (m); $m-1$ about total width of shell at level of opening of myostracum; $m+1$ wide, about equal in width to $m-1$, $m+2$ and 3 narrow (numbering following MacClintock, 1967).

Type Material: Holotype NHMW 2013/0566/0002, height 9.7 mm, diameter 34.0 mm \times 22.5 mm; paratype 1, NHMW 2013/0566/0001, height 16.9 mm, diameter



Figures 7–14. *Scutellastra* species. 7–9. *Scutellastra arayae* new species. Holotype SGO.PI.6650, height 55 mm, diameter $>93 \times 92.6$ mm. Punta Perro, lower Miocene Navidad Formation, central Chile. 10–14. *Scutellastra venezuelana* new species. From 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela, Cantaure Formation, upper Burdigalian-lower Langhian, lower-middle Miocene boundary. 10–11. Holotype NHMW 2013/0566/0002, height 9.7 mm, diameter $34.0 \text{ mm} \times 22.5 \text{ mm}$. 12–14. Paratype 1 NHMW 2013/0566/0001. Height 16.9 mm, diameter $60.5 \text{ mm} \times 43.0 \text{ mm}$.

60.5 mm \times 43.0 mm; paratype 2, NHMW 2013/0566/0003, height 10.6 mm, diameter 38.5 mm \times 27.8 mm; paratype 3, NHMW 2013/0566/0004, height 10.5 mm, diameter 40.3 mm \times 27.6 mm; paratype 4, NMB H20223, height 15.9 mm, diameter 62.0 mm \times 42.2 mm, NMB locality 17516; paratype 5, NMB H20224, height 14.7 mm, diameter 59.0 mm \times 43.2 mm, NMB locality 17516.

Type Locality: 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela, Cantaure Formation, upper Burdigalian-lower Langhian, lower-middle Miocene boundary.

Other Material Examined: Maximum dimensions: diameter 89.1 mm \times 58.7 mm. NHMW 2013/0566/0005 (8); NMB locality 17516 NMB (31 unnumbered specimens), same locality as type material.

Distribution: Only known from the type locality.

Etymology: Named after the country of origin, Venezuela. The gender of *Scutellastra* is feminine.

Measurements: Measurements follow Jerardino and Navarro (2008) of paratype 1. Total length (TL) 60.5 mm; anterior length (AL) 36.5 mm; posterior length (PL) 29.3 mm; total width (TW) 43.0 mm; lateral width (LW) 26.9 mm; anterior inner length (AIL) 20.3 mm; inner length (IL) 29.2 mm; posterior inner length (PIL) 12.7 mm; inner width (IW) 16.1 mm; lateral inner width (LIW) 16.8 mm.

Discussion: The rostration developed in *Scutellastra venezuelana* new species makes it superficially similar to the extant *Scutellastra cochlear* (Born, 1778) from the coasts of South Africa, but this species differs in having an even more pronounced rostration, which is somewhat pinched at the neck. Although this tendency to rostration is most strongly developed in *S. cochlear* and *S. venezuelana*, this character is probably convergent as it is developed to some degree in several other *Scutellastra* species; i.e. the eastern Pacific species *S. mexicana* (Broderip and Sowerby, 1829) and the Indo-Pacific species *S. optima* (Pilsbry, 1927). More importantly, *S. venezuelana* differs from both *S. cochlear* and *S. mexicana* in having coarser dorsal ribs, almost all of which are of primary strength, whereas both *S. cochlear* and *S. mexicana* have finer ribbing, with several orders of major and minor ribs.

Despite the superficial similarity between the shells of *S. cochlear* and *S. venezuelana*, there are no common factors between the Venezuelan and South African molluscan faunas, and the new Venezuelan species is much more likely to be related to the eastern Pacific *S. mexicana*. The similarity between these species is likely to be due to common ecological factors. According to Lindberg (2007), the tendency to rostration and an angular rather than rounded profile when viewed from the dorsal aspect are associated with gardening limpets that maintain the garden around the periphery of the shell. Lindberg (2007) suggested that the rostration might allow these limpets to

graze their gardens without leaving the vicinity of their home depressions.

Scutellastra venezuelana new species is quite unlike the Chilean *S. araya* new species, which is less flattened, the primary ribs are much broader and the shell does not develop the pronounced rostration so typical of *S. venezuelana*, *S. cochlear* and *S. mexicana*.

CONCLUSIONS

In the Recent American shallow marine faunas, *Scutellastra* is known only from the extant species *S. mexicana* occurring from West Mexico to Peru. This paper introduces two new species from the American fossil record. *Scutellastra araya* new species is the oldest and the southernmost record from the Americas. It is also the first patellid recognized from Cenozoic deposits of Chile. *Scutellastra venezuelana* new species is only slightly younger, straddling the early-middle Miocene boundary, it is the first record for the genus in the tropical American Neogene and the Caribbean/western Atlantic identified to species-level. This new record adds the genus *Scutellastra* to the list of Paciphile genera, i.e., genera which, following the closure of the Central American Seaway, disappeared from the Caribbean and became restricted to the Pacific side of their original wider distribution. For full list of Paciphile genera see Landau et al. (2009).

The biogeographic pattern of dispersal of patellid gastropods has been fairly controversial. This is not helped by the very poor fossil record for the group. "*Patella*" *soyaensis* Kase and Shigeta, 1996 from the upper Cretaceous of northern Japan, assigned to *Scutellastra* by Ridgway et al. (1998) is the oldest record for the genus, although the generic placement was questioned by Koufopanou et al. (1999). Together with the records from New Zealand, these new lower and lower-middle Miocene American records are among the oldest undisputed records for the genus. Koufopanou et al. (1999) suggested that *S. mexicana* was a relict from a formerly widespread Tethyan distribution of early *Scutellastra* species (Powell, 1973; Ridgway et al., 1998). They predicted that further *Scutellastra* should be discovered in the Atlantic and Mediterranean regions. These findings support their hypothesis.

Through comparison with the current biogeographic distribution of *Scutellastra* spp., as far as the Chilean record is concerned, it becomes evident that this fossil species is yet another piece of evidence that (1) shallow-water or, as in this case, even intertidal taxa were displaced into bathyal depth of the Navidad Formation (see Finger, 2013), (2) sea surface temperatures along the Chilean coast were significantly higher during the early Miocene than they are today (Nielsen and Glodny, 2009), and (3) discovery of this new species confirms the results of Kiel and Nielsen (2010) that, although the Navidad assemblage is relatively well described, there remain many more species to be discovered. The Venezuelan

record (1) illustrates again the importance of the Cantaure assemblage, as one of the very few tropical Neogene assemblages representing rocky bottom habitats (Vermeij, 2001; Landau et al., 2009; Landau and Vermeij, 2010), and (2) adds to the number of species known to have been distributed throughout the Neogene Gatunian province, but today restricted to the Panamie Pacific.

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LITERATURE CITED

- Adams, H. and A. Adams. 1853-1858. The genera of Recent Mollusca arranged according to their organisation. London: Van Voorst, 2 volumes of text, one volume of plates.
- Aguilera, O.A., H. Moraes-Santos, S. Costa, F. Ohe, C. Jaramillo, and A. Nogueira. 2013. Aroid sea catfishes from the coeval Pirabas (Northeastern Brazil), Cantaure, Castillo (Northwestern Venezuela), and Castilletes (North Colombia) formations (early Miocene), with description of three new species. *Swiss Journal of Palaeontology* 132: 45–68.
- Aguilera, O.A. and D. Rodríguez de Aguilera. 1999. Anormalidades esqueléticas en peces fósiles del Mioceno temprano (Formación Cantaure) de Venezuela. *Memoria Fundación La Salle de Ciencias Naturales* 59(151): 45–52.
- Anderson, L.C. and P.D. Roopnarine. 2005. Role of constraint and selection in the morphologic evolution of *Caryocorbula* (Mollusca: Corbulidae) from the Caribbean Neogene. *Palaeontologia Electronica*, Article 8.2.32A.
- Beu, A.G. and P.A. Maxwell. 1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey, *Palaeontological Bulletin* 58: 1–518.
- Blow, W.H. 1969. Late Middle Eocene to Recent Planktonic Foraminiferal Biostratigraphy. *Proceedings of the First International Conference on Planktonic Microfossils*, Geneva, 1967, 1: 199 pp.
- Bolli, H.M., 1966. Zonation of Cretaceous to Pliocene marine sediments based on planktonic foraminifera. *Asociación Venezolana de Geología, Minería y Petróleo, Boletín Informativo* 9(1): 3–32.
- Born, I. von. 1778. *Index Rerum Naturalium Musei Caesarei Vindobonensis Pars I. Testacea. Verzeichniss etc.* Illust. Vindobonae, 458 pp.
- Bouchet, P. and J.-P. Rocroi. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47: 1–397.
- Broderip W.J. and G.B. Sowerby I. 1829. Observations on new or interesting Mollusca contained, for the most part, in the Museum of the Zoological Society. *Zoological Journal* 4: 359–379, pl. 9.
- DeVries, T.J. 2008. Cenozoic *Nacella* (Patellogastropoda: Nacellidae) from Peru and Chile: Filling in the gaps. *The Veliger* 50: 274–291.
- DeVries, T.J. and D. Frassinetti. 2003. Range extensions and biogeographic implications of Chilean Neogene mollusks found in Peru. *Boletín del Museo Nacional de Historia Natural, Chile* 52: 119–135.
- Díaz de Gamero, M.L. 1974. Microfauna y edad de la Formación Cantaure, Península de Paraguaná, Venezuela. *Asociación Venezolana de Geología, Minería y Petróleo, Boletín Informativo* 13: 41–47.
- Encinas, A., J.P. Le Roux, L.A. Buatois, S.N. Nielsen, K.L. Finger, E. Fourtanier, and A. Lavenue. 2006. Nuevo esquema estratigráfico para los depósitos mio-pliocenos del área de Navidad (33°00'–34°30' S), Chile central. *Revista Geológica de Chile* 33: 221–246.
- Espoz, C., D.R. Lindberg, J.C. Castilla, W.B. Simison. 2004. Los patelogastrópodos intermareales de Chile y Perú. *Revista Chilena de Historia Natural* 77: 257–283.
- Finger, K.L. 2013. Miocene foraminifera from the south-central coast of Chile. *Micropaleontology* 59: 341–492.
- Finger, K.L., S.N. Nielsen, T.J. DeVries, A. Encinas, and D.E. Peterson. 2007. Paleontologic evidence for sedimentary displacement in Neogene forearc basins of Central Chile. *Palaios* 22: 3–16.
- Fleming, C.A. 1973. Kermadec Island giant limpet occurring fossil in New Zealand, and relict distributions in the tropics. *New Zealand Journal of Marine and Freshwater Research* 7: 159–164.
- González-Wevar, C.A., T. Nakano, J.I. Cañete, and E. Poulin. 2011. Concerted genetic, morphological and ecological diversification in *Nacella* limpets in the Magellanic Province. *Molecular Ecology* 20: 1936–1951.
- Gradstein, F.M., J.G. Ogg, M.D. Schmitz, and G.M. Ogg. 2012. *The Geologic Time Scale 2012*. Elsevier, Amsterdam, vol. 2, pp. 437–1144.
- Griffin, M. and S.N. Nielsen. 2008. A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by d'Orbigny (1842), Sowerby (1846), and Hupé (1854). *Journal of Systematic Palaeontology* 6: 251–316.
- Griffiths, N., W. Müller, K.G. Johnson, and O.A. Aguilera. 2013. Evaluation of the effect of diagenetic cements on element/Ca ratios in aragonitic Early Miocene (~16 Ma) Caribbean corals: Implications for 'deep-time' palaeoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 369: 185–200.
- Herm, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. *Zitteliana* 2: 1–159.
- Hunter, V.F. and P. Bartok. 1974. The age and correlation of the Tertiary sediments of the Paraguaná Península, Venezuela. *Asociación Venezolana de Geología, Minería y Petróleo, Boletín Informativo* 17: 143–154.
- Ibaraki, M. 1992. Planktonic foraminifera from the Navidad Formation, Chile: their geologic age and paleoceanographic implications. In: Ishizaki K. and T. Saito (eds.) *Centenary of Japanese Micropaleontology*. Terra Scientific Publishing Company, Tokyo, pp. 91–95.
- Jerardino, A. and R. Navarro. 2008. Shell morphometry of seven limpet species from coastal shell middens in southern Africa. *Journal of Archaeological Science* 35: 1023–1029.
- Jung, P. 1965. Miocene Mollusca from the Paraguaná Peninsula, Venezuela. *Bulletins of American Paleontology* 49(223): 387–644.
- Kase, T. and Y. Shigeta. 1996. New species of Patellogastropoda (Mollusca) from the Cretaceous of Hokkaido, Japan and Sakhalin, Russia. *Journal of Paleontology* 70: 762–771.
- Kiel, S. and S.N. Nielsen. 2010. Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology* 38: 955–958.

- Koufopanion, V., D.G. Reid, S.A. Ridgway, and R.H. Thomas. 1999. A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution* 11: 138–156.
- Lamarck, J.B.P.A. de M. de. 1819. Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leurs distributions, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction... Vol. 6. Paris, "chez l'auteur, au jardin du Roi". vi + 343 + 232 pp.
- Landau B.M. and G.J. Vermeij. 2010. A new species of *Plicopurpura* (Mollusca: Rapaninae) from the Lower Miocene Cantaure Formation of Venezuela. *Novapex* 11: 99–106.
- Landau, B.M., G.J. Vermeij, and C.M. da Silva. 2009. Pacific elements in the Caribbean Neogene gastropod fauna: the source-sink model, larval development, disappearance, and faunal units. *Bulletin de la Société Géologique de France* 180: 249–258.
- Le Roux, J.P., S.N. Nielsen, H. Kemnitz, and A. Henriquez. 2008. A Pliocene mega-tsunami deposit and associated features in the Ranquil formation, southern Chile. *Sedimentary Geology* 208: 164–180.
- Léxico Estratigráfico de Venezuela (L.E.V.) 1997. Léxico Estratigráfico de Venezuela. Ministerio de Energía y Minas. Tercera Edición. Boletín Geológico 12: 1–828. Available online at <http://www.pdv.com/lexico/c19w.htm>, accessed 07.04.2014.
- Lindberg, D.R. 1998. Order Patellogastropoda. In: Beesley, P.L., G.J.B. Ross and A. Wells (eds.), *Mollusca: The Southern Synthesis. Fauna of Australia*. Vol. 5. Melbourne: CSIRO Publishing. pp. 639–652.
- Lindberg, D.R. 2007. Reproduction, ecology, and evolution of the Indo-Pacific limpet *Scutellastra flexuosa*. *Bulletin of Marine Science* 81: 219–234.
- Lindberg, D.R. and C.S. Hickman. 1986. A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). *Journal of Paleontology* 60: 661–668.
- Linnaeus, C. 1758. *Systema Naturae*, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10 ed. Holmiae: Laurentii Salvii, 2 volumes, 1384 pp.
- Martini, E. 1971. Standard Tertiary and Quaternary Calcareous Nannoplankton Zonation. In: Farancini, A. (ed.) *Proceedings of the II Planktonic Conference*, Rome, 1970, Ed. Tecnosci., 2: 739–785.
- MacClintock, C. 1967. Shell structure of patelloid and bellerophonid gastropods (Mollusca). *Bulletins of the Peabody Museum of Natural History* 22: 1–140.
- Monterosato, T.A. di. 1884. *Conchiglie litorali mediterranee*. *Il Naturalista Siciliano* 3: 102–111.
- Montfort, P.D.D. 1810. *Conchylologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues*. F. Schoell, Paris, 2, 676 pp.
- Nakano, T. and T. Ozawa. 2007. Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and paleontological evidence. *Journal of Molluscan Studies* 73: 79–99.
- Nielsen, S.N. and J. Glodny. 2009. Early Miocene subtropical water temperatures in the southeast Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280: 480–488.
- Nolf, D. and O. Aguilera. 1998. Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 68: 237–262.
- Powell, A.W.B. 1938. Tertiary molluscan faunules from the Waitemata beds. *Transactions of the Royal Society of New Zealand* 68: 362–379.
- Powell, A.W.B. 1973. The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3(15): 75–200.
- Quoy, J.C.R. and P. Gaimard. 1834. *Voyage de découvertes de l'Astrolabe, exécuté par ordre du Roi pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville*. Mollusques. *Zoologie*, Tome 3, 1–366.
- Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palerme, 223 pp.
- Reeve, L.A. 1854. Monograph of the genus *Patella*. *Conchologia Iconica* 8: pls. 2–24.
- Rey, O.T. 1996. Estratigrafía de la Península de Paraguaná, Venezuela. *Revista de la Facultad Ingeniería de Venezuela* 11: 35–45.
- Ridgway, S.A., D.G. Reid, J.D. Taylor, G.M. Branch, and A.N. Hodgson. 1998. A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda). *Philosophical Transactions of the Royal Society London B* 353: 1645–1671.
- Tenison-Woods, J.E. 1876. Description of new Tasmanian shells. *Papers and Proceedings and Report of the Royal Society of Tasmania* 1875: 134–160.
- Valdovinos, C. and M. Rùth. 2005. Nacellidae limpets of the southern end of South America: taxonomy and distribution. *Revista Chilena de Historia Natural* 78: 497–517.
- Vermeij G.J. 2001. Distribution, history, and taxonomy of the *Thais* clade (Gastropoda: Muricidae) in the Neogene of tropical America. *Journal of Paleontology* 75: 697–705.
- Watters, W.A., and C.A. Fleming. 1972. Contributions to the geology and paleontology of Chiloe Island, southern Chile. *Philosophical Transactions of the Royal Society of London B* 263: 369–408.
- Wenz, W. 1938–1944. *Gastropoda*. Teil 1, Allgemeiner Teil und Prosobranchia. In Schindewolf, O.H. (ed.), *Handbuch der Paläozoologie*. Vol. 6. Berlin: Gebrüder Bornträger, 1639 pp.

The family Caecidae (Gastropoda: Caenogastropoda) in Argentine waters

Guido Pastorino

Ignacio Luis Chiesa

Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”
Av. Ángel Gallardo 470
C1405DJR Ciudad Autónoma de Buenos Aires, ARGENTINA
gpastorino@macn.gov.ar

ABSTRACT

This is the first formal report of members of the family Caecidae in Argentine waters. *Caecum striatum* de Folin, 1868, *C. strigosum* de Folin, 1868, and *C. achirona* (de Folin, 1867) are re-described from shallow waters off Piedras Coloradas (~40°53.081' S, 65°07.592' W), Río Negro Province, Argentina. This is the farthest south record of these species which were previously recorded from USA, Bahamas, Panama, Brazil, and Uruguay. The authors also make observations about the different ontogenetic stages of the studied species. Scanning electron microscope illustrations of radula and operculum are provided for the first time.

Additional Keywords: Argentina, *Caecum*, Patagonia, taxonomy

INTRODUCTION

The family Caecidae comprises marine caenogastropods with simple cylindrical (Caecinae) or almost planispiral (Ctiloceratinae) very small shells, usually around 2–3 mm which in rare cases are larger than 5 mm. The Caecinae inhabit tropical and temperate environments, mostly in shallow waters. The early works of Carpenter (1858) and de Folin (1877) established that at least three different growth stages are present in representatives of the group. However, Bandel (1996) reported more complicated arrangements, which may be unique for each species.

Probably because of small size, particular ontogeny, and somewhat conservative shell morphology, the taxonomy of this interesting group is far from complete. In addition, most of the species have been described based solely on shell characters. However, some earlier workers (e.g., Gotze, 1938; Marcus and Marcus, 1963; Draper, 1979; Bandel, 1984; etc.) described the radular morphology of some species. Marcus and Marcus (1963) presented drawings of the anatomy, operculum, and radulae of what they identified as *C. corneum* and *C. pulchellum* from the littoral of São Paulo, Brazil. The actual identities of these species are need of revision.

The first descriptions of species of *Caecum* from the southwestern Atlantic are those of de Folin (1868; 1874) as reported by Klappenbach (1964). Later, Lange de Morretes (1954) described a new species from São Paulo State, which, together with his previous list (1949) increased the number of species of Caecinae known from Brazil.

These former workers are pioneers in the study of this complex family; however, only in more recent years the revision of type specimens led to a better understanding of the identities of those nominal species. Absalão (1994; 1995; 1997), Gomes and Absalão (1996), and Absalão and Gomes (2001) made the first attempts, using modern criteria, to review the family in the southwestern Atlantic.

More recently, Lima et al. (2013) improved on the traditional format of species descriptions with an ontogenetic approach that we attempted to follow here. Lima et al. (op. cit.) reported more than 30 species living along Brazilian coast.

In the other countries of southern South America other than Brazil, recent species of Caecidae have been described from Chile (Stuardo, 1962; 1970; Di Geronimo et al., 1995) and Uruguay (Klappenbach, 1964; Scarabino, 2004). Farinati (1994) reported the presence of *Caecum antillarum* Carpenter, 1858 from Holocene deposits from Bahía Blanca, Buenos Aires Province, Argentina. In addition, Penchaszadeh (1973) cited the presence of *Caecum* sp. as part of the diet of the sea star *Astropecten brasiliensis* collected off Buenos Aires Province. The latter, as far as we know, constitutes the only published report of recent members of the family Caecidae from Argentina.

In this paper we describe, for the first time, three recent representatives of this intriguing family from Argentine waters. The study includes SEM illustrations of the radulae, opercula, and remarks on the ontogeny of some of these species.

MATERIALS AND METHODS

The material described herein was collected during a sampling project focused essentially on small peracarid

Table 1. Localities where specimens of *Caecum* were found. (s= starting, and e= ending point).

Station number	Sediment	Fishing gear	Latitude	Longitude	Depth (m)
4	Fine sand	van Veen grab	40°53.515' S	65°04.166' W	15
5	Medium sand	van Veen grab	40°53.863' S	65°04.533' W	18
6	Medium/ fine sand	van Veen grab	40°54.135' S	65°05.074' W	15
15	Medium sand	Rauschert sledge	s: 40°55.728' S e: 40°53.141' S	65°04.317' W 65°04.396' W	15
18	Extra fine sand	van Veen grab	40°54.579' S	65°06.307' W	12
19	Fine sand	van Veen grab	40°55.208' S	65°03.983' W	18

crustaceans from shallow waters in San Matías Gulf, Río Negro, Argentina, during January of 2005. The samples were obtained using a van Veen grab and a Rauschert sledge, deployed from a small boat in several stations off Piedras Coloradas (40°53.081' S, 65°07.592' W). The grab area was 0.05 m². The sledge opening measured 55 × 15 cm and was equipped with nylon net of 1 × 1 mm mesh size. The samples were manually sieved 10 times, and then the sorted material was fixed with formalin 4% on sea water, and later preserved in 70% ethanol. Table 1 lists the stations where Caecidae were present, including the fishing gear, geo-referenced locality, depth, and sediment grain size.

Due to small size, radulae were taken dissolving the whole animal on a hanging drop slide with sodium hypochlorite. Once clean, the radula was moved to another slide filled with distilled water in which a piece of photographic film was glued to the bottom of the cavity with the emulsion side up. Once the water evaporated, the film was removed and attached to a SEM stub, and coated with gold-palladium. Shells were cleansed in an ultrasonic cleaner and observed and photographed under SEM at the Museo Argentino de Ciencias Naturales (MACN).

The genus *Caecum* sensu lato usually develops a deciduous and spiral protoconch. The protoconch is generally lost and a septum closes off the first stage of the teleoconch. This latter could be ornamented with a structure more or less developed (finger-like, flat, subquadrate, etc.) called *mucro*. Sometimes the mucro pierces the septum and is clearly distinguishable as in Figures 4–8, or could be less differentiated, as in Figures 12–15. The teleoconch could develop several ontogenetic stages, herein referred to, if the protoconch is present, as stages I, II, III, and so on, or, if the protoconch is lacking, as stages X, Y, Z, etc. The ontogenetic stages of the teleoconch could be still attached, in which case a fracture line is visible.

The material is housed at the invertebrate collection of the MACN.

RESULTS

Six of the 21 samples contained several specimens of three different species of Caecidae in different ontogenetic stages. *Caecum striatum* de Folin, 1868 was the commonest and the other species, *C. strigosum* de Folin, 1868 and *C. achirona* (de Folin, 1967) appear to be rare.

The sediment where this fauna live is mainly sand of medium and fine grain. They were found between 12–18 m depth, most of them alive and associated with different species of amphipods, mainly belonging to species in the family Phoxocephalidae.

SYSTEMATICS

Family Caecidae Gray, 1850

Subfamily Caecinae Gray, 1850

Genus *Caecum* Fleming, 1813

***Caecum striatum* de Folin, 1868**

Figures 1–25

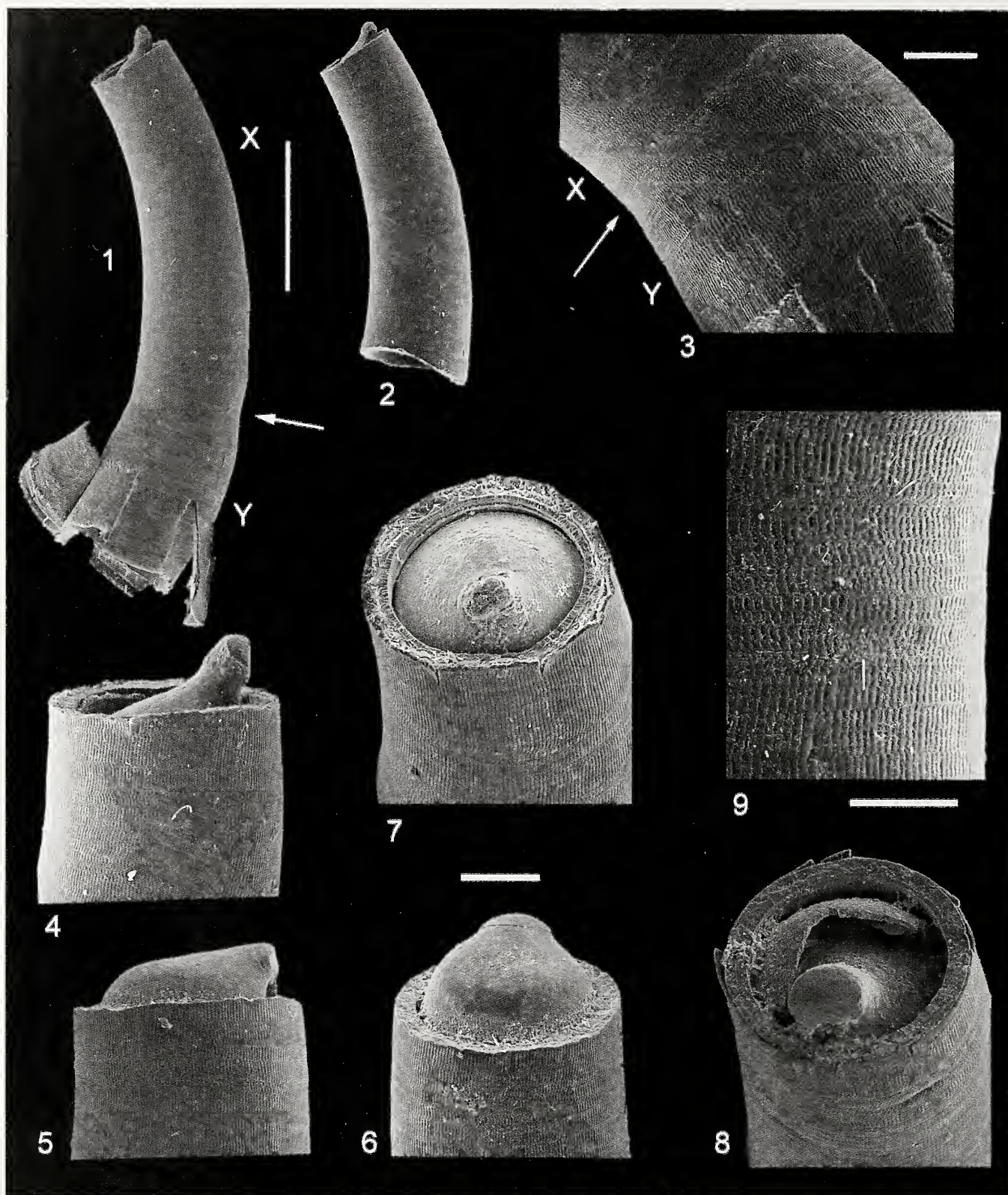
Caecum striatum (de Fol.)—de Folin, 1868: 49, pl. 5, fig.3; Rios, 1994: 56, pl. 18, fig. 207; Gomes and Absalão, 1996: 519, fig. 7; Absalão and Gomes, 2001: 12, figs. 8–9 (lectotype designated).

Caecum striatum, var. *obsoleta* de Folin, 1874: 212.

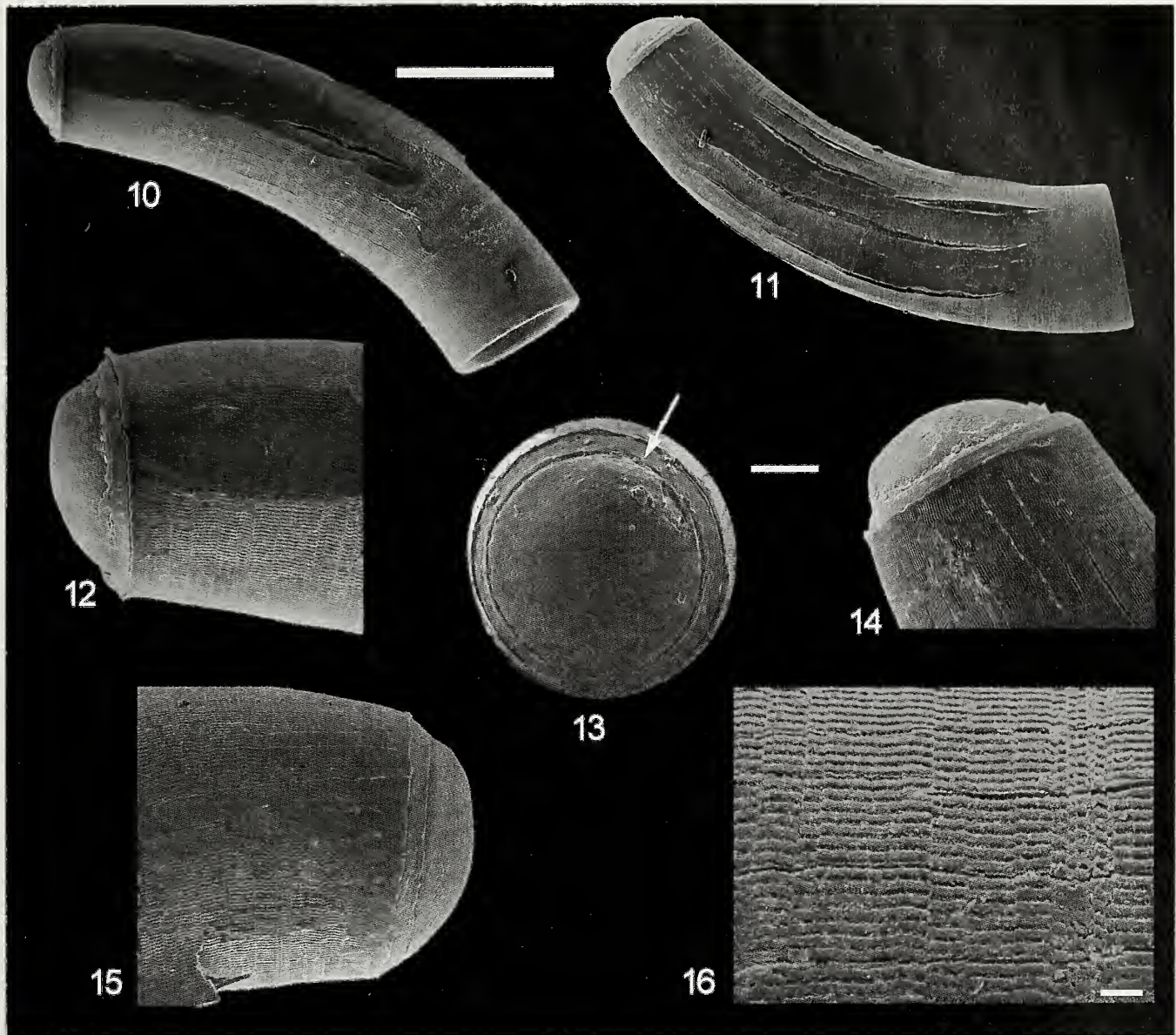
Caecum antillarum Carpenter, 1857. —Rios, 1994: 56, pl. 18, fig. 203.

Description: SHELL: Protoconch unknown. Teleoconch X (first stage) very small, less than 1.5 mm; tubular, slightly and regularly curved; apical caliber somewhat larger than apertural; periostracum translucent-brownish, thick, brittle when dry, covered with longitudinal microscopic (but visible under stereoscopic microscope), close-spaced, continuous, weakly sinuous striae; shallow thin grooves among striae, faint circular lines (growth lines?) crossing striae and producing wavy ends to those striae. Septum flat to slightly convex; mucro thin, finger-shaped, weakly projected, flat; rising from the interior covered by septum, sometimes partially broken (Figure 8), positioned on dorsal margin. Teleoconch Y (second stage) (Figures 1 and 3 show the starting point indicated by a sudden increase in diameter thickening) small, about 1.5 mm, moderately curved; apertural diameter slightly larger than apical; apical region circular, with slight constriction; rounded hemispheric septum, with flat, polygonal dorsal mucro, slightly twisted to left, sometimes very weak; oblique rim always present between septum and end of striae; septum and mucro whitish. This was the most abundant stage found.

RADULA (Figures 17–18): Rachidian tooth somewhat semicircular in outline, with 12–13 short cusps, the central larger than lateral cusps; lateral teeth with 12–13 short



Figures 1-9. Teleoconch of *Caecum striatum* de Folin, 1868. **1.** MACN-In 39530-1, Teleoconch X and Y, showing the periostracum broken, arrow heads probable fracture line between two ontogenetic stages, X and Y. **2.** MACN-In 39530-2. Scale bar = 500 μ m. **3.** Detail of Figure 1 showing the probable fracture line between two ontogenetic stages. Scale bar = 100 μ m. **4-8.** Five lateral views of septum and mucro. **4.** Detail of specimen in Figure 1. **5-6.** MACN-In 39530-3. **7.** MACN-In 39530-4. **8.** MACN-In 39530-5. Scale bar = 100 μ m. **9.** Detail of the ornamentation of the shell of the specimen in Figure 2. Scale bar = 50 μ m.



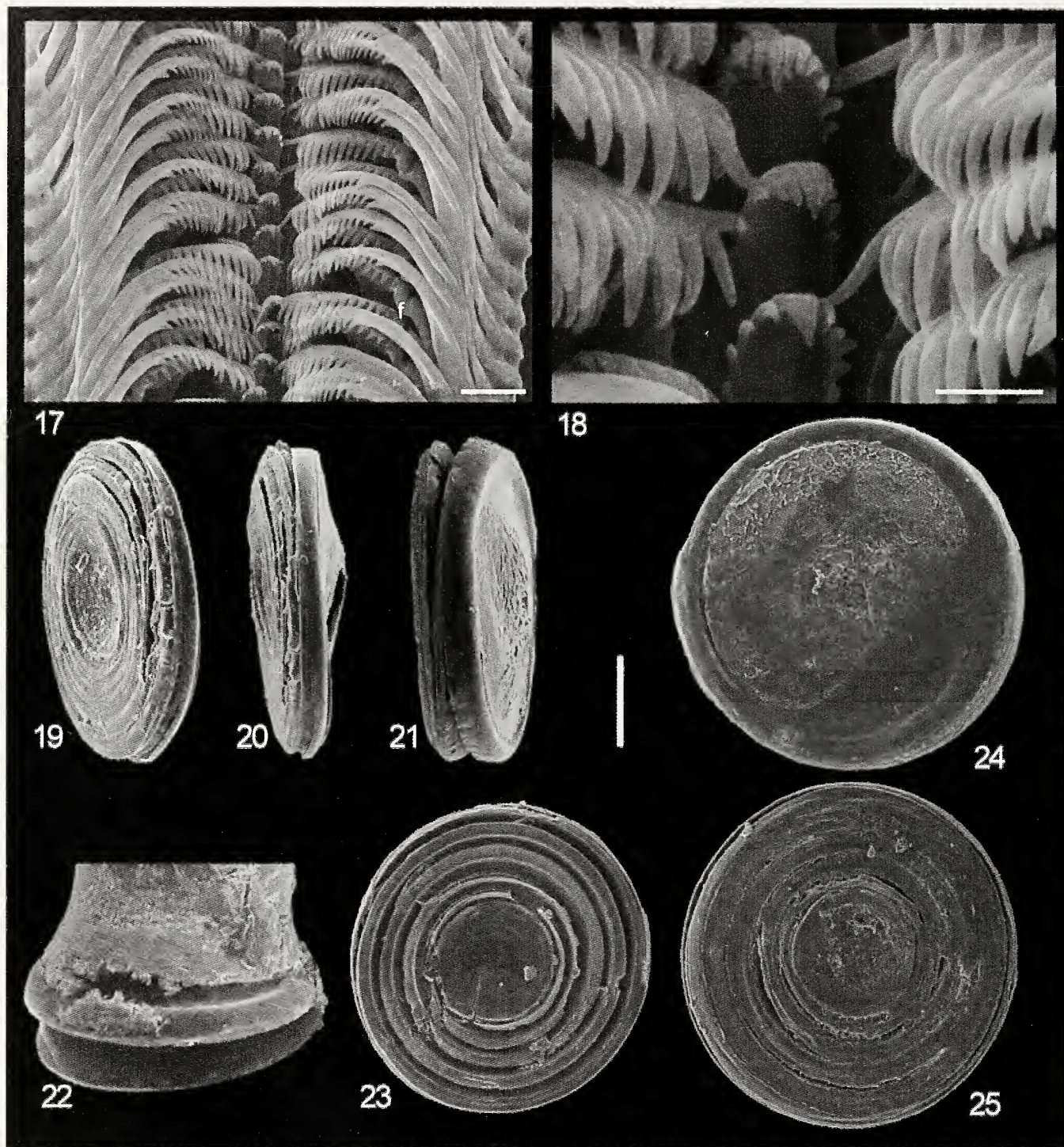
Figures 10–16. Teleoconch of *Caecum striatum* de Folin, 1868. **10.** MACN-In 39531-1, teleoconch. **11.** MACN-In 39531-2, teleoconch, showing the periostracum broken. Scale bar = 500 μ m. **12–15.** Four different views of septum and mucro of different specimens. **12.** Detail of apical extreme of Figure 10. **13.** MACN-In 39531-3, Detail of septum and mucro, arrow heads mucro. **14.** Detail of the apical extreme of specimen in Figure 11. **15.** Lateral view of the apical extreme of specimen in Figure 13. Scale bar = 100 μ m. **16.** Detail of the ornamentation of the shell in Figure 15. Scale bar = 20 μ m.

cusps, larger than those of rachidian and smaller than those of inner marginal teeth; inner marginal tooth long, larger than all others, with 12–15 large, sharp cusps; at end of cusps, a deep furrow (f) shows the starting point of the long tooth stalk; outer marginal long, slender, with 12–14 cusps smaller than those of inner marginal tooth. Radulae show similar features at all the growth stages.

OPERCULUM (Figures 19–25): Similar in all growth stages, circular, thick, corneous, external surface slightly and mainly in the center concave, multispiral, sculptured with a thick subquadrate cord of 4–5 whorls, separated by

a deep furrow, sometimes partially covered; internal surface convex, attachment area spanning half of total surface, small central hole present; internal and external surface closely attached; margin of inner surface reflected over outer surface and covering its margin.

Material Examined: MACN-In 39535, St.5; MACN-In 39533, St. 6; MACN-In 39532, St. 15; MACN-In 39534 St. 19; MACN-In 39536, St. 18; MACN-In 39530/1–5 (illustrated specimens); St. 18; MACN-In 39531/1–3 (illustrated specimens), St. 18; all off Piedras Coloradas, San Matías Gulf, Río Negro Province, Argentina.



Figures 17–25. Radula and operculum of *Caecum striatum* de Folin, 1868. 17. Dorsal view of the radula, scale bar = 5 μm . 18. Detail of the rachidian tooth, scale bar = 2 μm . 19–25. Operculum. 19. Twisted external view. 20. Side view. 21. Twisted internal view. 22. Operculum attached, critical point dried. 23. External view. 24. Internal view. 25. External view with furrows uncovered. Scale bar = 100 μm . Abbreviation: f, furrow in the inner marginal tooth.

Distribution: Florida, USA; Bahamas; West Indies (according to Lightfoot, 1992); Panama; Pernambuco state, Fernando de Noronha Is., Rio de Janeiro, Brazil (according to Leal, 1991; Absalão and Gomes, 2001 (as *C. strigosum*)) and Río Negro, Argentina.

Remarks: Two ontogenetic stages (X and Y) are attributed to this species. As no complete or united specimen was found, the ontogenetic order was arranged according to the diameter of the aperture and septum area of each stage and the general morphology of the shell. The

stage Y is the usually described form; however, the most abundant stage was stage X.

Absalão and Gomes (2001) designated lectotypes of *C. striatum* and *C. strigosum* and opened the discussion about the possibility of these two names being synonyms. We found enough distinction to maintain the two species separate until more information is available.

There is a series of errors on the publication dates of the two species. Previous authors (i.e., Rios, 1985; 1994; Leal, 1991; Ligthfoot, 1992; Absalão and Gomes, 2001) considered 1867 as the publication date of *C. strigosum*. Rehder (1946) completed the collation of de Folin's "*Les Fondes de la Mer*" previously published by Winkworth (1941). According to them, both descriptions, from the first volume of this work, were published in 1868.

***Caecum strigosum* de Folin, 1868**

Figures 26–34

Caecum strigosum (de Fol.)—de Folin, 1868: 53, pl. 5, fig. 51869; : 261;

Caecum strigosum de Folin, 1867. —Rios, 1985: 44, fig. 194; 1994: 57, pl. 18, fig. 208; Leal, 1991: 86, pl. 13, figs. H–I; Ligthfoot, 1992: 28, fig. 31; Absalão and Gomes, 2001: 11, figs. 7, 8.

Description: Protoconch unknown; teleoconch medium sized, tubular, slightly curved, about 2 mm with a clear, somewhat oblique, swelling, right at the end of the aperture; sculptured with longitudinal striae, sometimes obsolete, similar to those described for *C. striatum* but shallower, thinner and with more wavy pattern; septum evenly curved, hemispherical, without rim, protruded; mucro small, sometimes very weak or obsolete, twisted to left (Figure 32).

Radula similar to that of *C. striatum*. Operculum similar to *C. striatum* but the attachment area at the internal surface is smaller (Figure 34).

Material Examined: MACN-In 39537, St. 4; MACN-In 39538/1–4, St.18, all off Piedras Coloradas, San Matías Gulf, Río Negro Province, Argentina.

Distribution: According to Rios (2009), from Maranhão to São Paulo, Brazil; however, this author considers *C. striatum* as a synonym. The distribution of both species may overlap.

Remarks: According to Absalão and Gomes (2001) *C. striatum* and *C. strigosum* should be treated as synonyms. No doubts both species are really closer. However, the presence of the apertural swelling in *C. strigosum* together with the hemispherical septum and the almost obsolete mucro clearly separates the latter species. In addition, the smaller attachment area of the operculum of *C. striatum* adds to the separation of the two species. However, it still remains to be investigated whether these differences represent just steps in the ontogeny of a single species.

***Caecum achirona* (de Folin, 1867)**

Figures 35–49

Brochina achirona de Folin, 1867: 57, pl. 3, fig.1.

Caecum achironum de Folin, 1867. —Absalão and Gomes, 2001: 13, figs. 20, 21 (lectotype designation).

Description: SHELL (Figures 35–44): Protoconch planispiral with one whorl, translucent, vitreous, with several very weak, faint cords on a crinkly surface; transition to teleoconch I well defined. Teleoconch I and II of similar, short length, with a weak increase in diameter; transition to teleoconch II appears as slight constriction; two other constrictions are also apparent. Teleoconch X short, ~1/3 length of teleoconch Y; transition to teleoconch Y shown as an increase in diameter; teleoconch Y large, strong. Septum large, dome- or finger-shaped, thick, flattened above, lower part somewhat oblique; mucro not visible. Complete shell (X+Y) moderately large, about 2.5 mm in length, curved, tapering toward the end, strong; anterior diameter twice as large as posterior one; shell translucent; aperture circular, with sharp lip. Shell surface smooth covered with fine growth lines only visible under SEM; periostracum whitish, translucent, very thin.

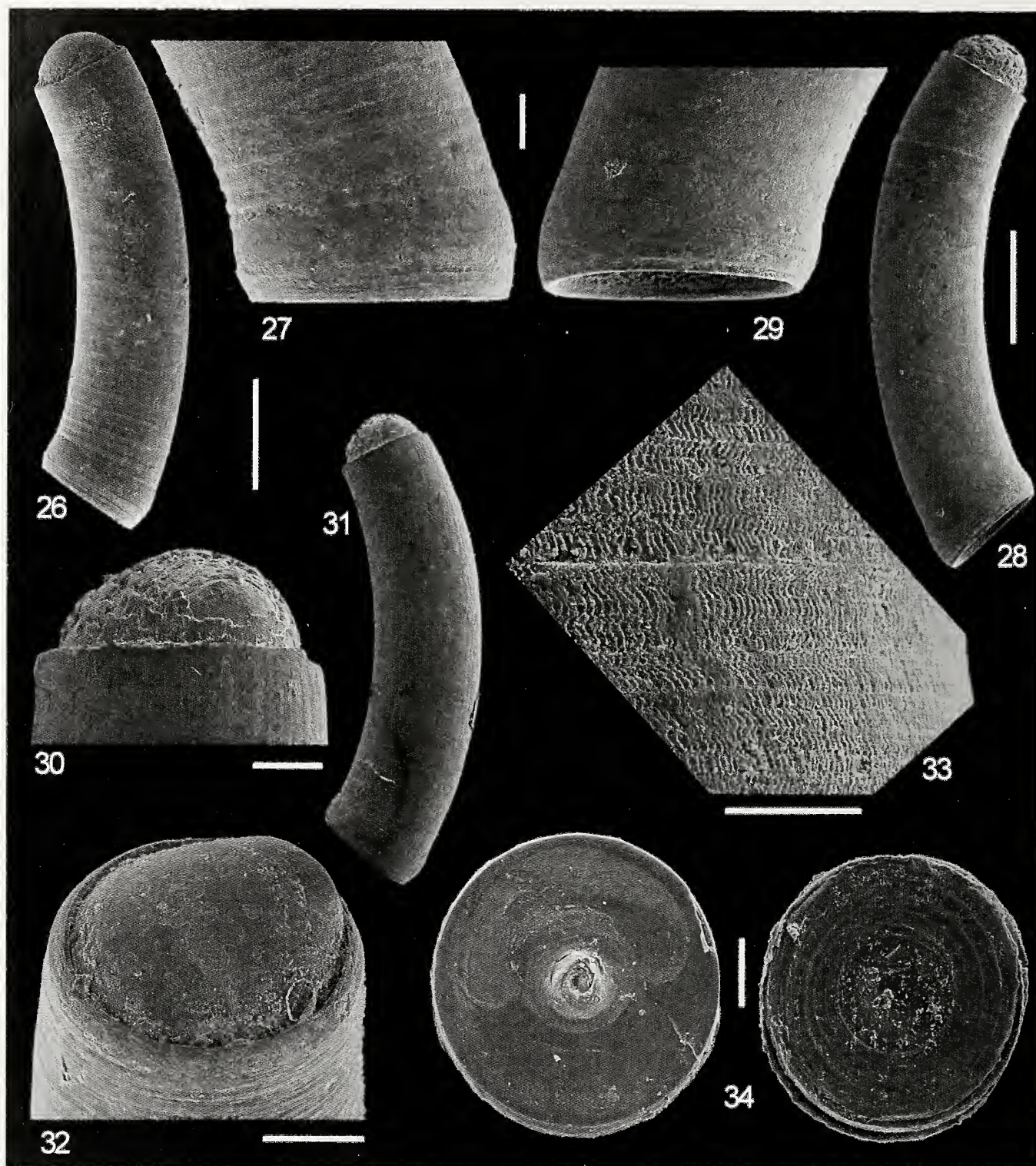
RADULA (Figures 45–46): Rachidian tooth small, flattened, outline semicircular, with ~10 very small cusps; lateral tooth small, visible behind inner marginal, with about 12 small cusps larger than the rachidian tooth cusps; inner marginal tooth thick, strong, with about 6 thick, strong, rectangular cusps, larger than the cusps of rachidian and marginal teeth, a deep furrow present at the end of the cusps lateral tooth (f in Figure 43); outer marginal tooth long, slender, thin, with 10–12 small and sharp cusps.

OPERCULUM (Figures 47–49): Circular, thick, with the external surface slightly concave, with a thick spiral cord, covered; internal surface convex, attachment area appears to cover the whole surface, a central hole at the center of the spiral formed by the margin of the spring; margin of the inner surface is reflexed covering the margin of the outer surface.

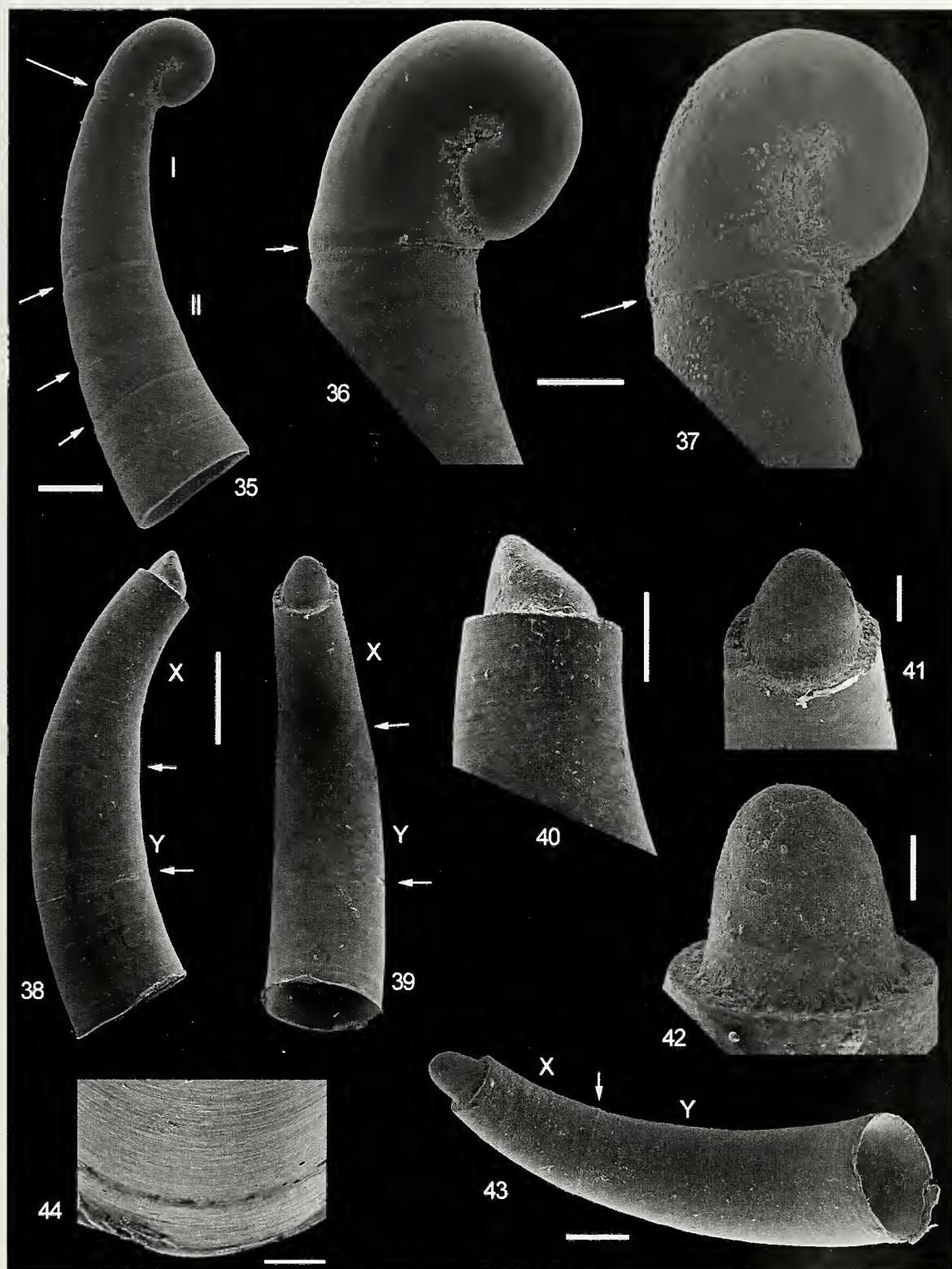
Material examined: MACN-In 39529/1–4, St. 5, off Piedras Coloradas, San Matías Gulf, Río Negro Province, Argentina.

Distribution: The actual distribution of this species is hard to know as it is difficult to ascertain the taxonomic circumscription of the nominal species treated by different authors. The species has been apportioned to north-eastern Brazil (Pernambuco and Bahia states) by de Folin (1867). Ligthfoot (1992) reported it from Tobago and Uruguay; it was however not mentioned by Scarabino (2004; Uruguay).

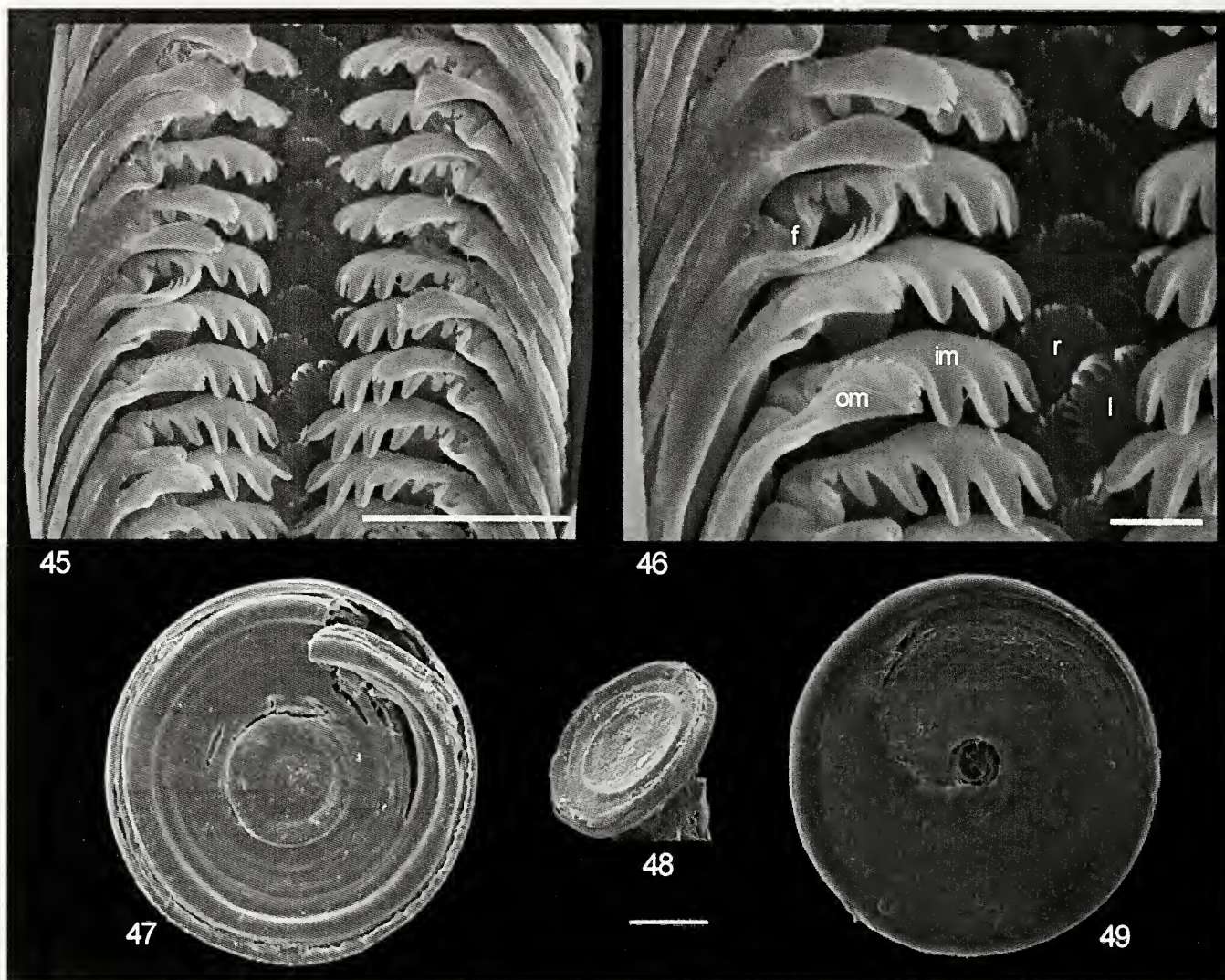
Remarks: There are some morphological differences between the material of *Caecum achirona* described here and the lectotypes illustrated by Absalão and Gomes (2001), particularly the "longitudinal microstriation,"



Figures 26–34. *Caecum strigosum* de Folin, 1868. 26. MACN-In 39538-1, scale bar = 500 μ m. 27. Detail of the swelling around the aperture in Figure 26. Scale bar = 100 μ m. 28. MACN-In 39538-2. Scale bar = 500 μ m. 29. Detail of the swelling around the aperture in Figure 28. Scale bar = 100 μ m. 30. Apical view of the septum and mucro of specimen in Figure 31. Scale bar = 100 μ m. 31. MACN-In 39538-3, scale bar same in Figure 26. 32. MACN-In 39538-4, apical view of septum and mucro. 33. Detail of the ornamentation of the teleoconch of specimen in Figure 28. Scale bar = 50 μ m. 34. Internal and external view of the operculum. Scale bar = 100 μ m.



Figures 35–44. *Caecum achirona* (de Folin, 1867). **35.** MACN-In 39529-1, protoconch, still attached to teleoconch I and II, arrows head probable fracture point. Scale bar = 200 μ m. **36.** Detail of the protoconch of Figure 35, arrow heads the boundary edge with teleoconch. Scale bar= 100 μ m. **37.** MACN-In 39529-2, protoconch. Scale bar same as for Figure 36. **38–39.** MACN-In 39529-3, two views of teleoconch X and Y, arrows head the probable fracture point, scale bar = 500 μ m. **40–41.** Details of the septum of Figures 38 and 39. Scale bars: 40= 200 μ m, 41=100 μ m. **42.** MACN-In 39529-4, detail of the septum from Figure 43. Scale bar = 50 μ m. **43.** MACN-In 39529-4, teleoconch x and y, arrow heads probable fracture point. Scale bar = 200 μ m. **44.** Detail of the surface of the shell. Scale bar = 100 μ m.



Figures 45–49. *Caecum achirona* (de Folin, 1867). Radula and operculum. **45.** Dorsal view of the radula, scale bar = 20 µm. **46.** Detail of the lateral teeth, scale bar = 5 µm. Abbreviations: **f**, furrow; **im**, inner marginal tooth; **l**, lateral tooth; **om**, outer marginal tooth; **r**, rachidian tooth. **47–49.** Three views of the operculum. **47.** External view. **48.** Twisted view, still attached. **49.** Internal view. Scale bar = 100 µm.

which, according to these authors, characterizes the species. All the specimens studied here are smooth. This ornamentation appears to be a variable character (F. B. Lima, *in litt.*), all other features allocated the material into *C. achirona*. In addition, the differences with *C. someri* de Folin, 1867 are also not clear. Absalão and Gomes (2001) designated lectotypes of the latter and considered both as different species. According to the illustrations in Absalão and Pizzini (2002, pl. 4, figs. 30–32) the shell in *C. someri* presents an apertural constriction that is absent in *C. achirona*.

"Fartulum" magellanicum Di Geronimo, Privitera, and Valdovinos, 1995 from the Pacific entrance of the Strait of Magellan in about 100 m depth, is vaguely similar. This latter species is smaller in size, reaching not more than 2 mm of shell length, the septum is blunter and the aperture margin is somewhat reflected.

Also, the protoconch appears to be the same diameter all along the entire whorl, while the Atlantic species is smaller in the first half. Gauging from the number of individuals found, *Caecum achirona* is a locally uncommon species.

DISCUSSION

The study of the family Caecidae from the southwestern Atlantic is far from complete. The particular shell morphology with several ontogenetic stages and variable ornamentation (Absalão and Pizzini, 2002), small size, and the stereotyped original illustrations are probably altogether responsible for this scenario. In addition, most of the papers written so far described only the shell, with more or less details. Radular characters are usually not

included (but see Marcus and Marcus, 1963; Draper, 1979; Bandel, 1984). Even when radular characters are included the rare it is difficult to determine taxonomic relationships. In the material studied here, the morphology of the radula of *C. striatum* and *C. strigosum* clearly differs from that of *C. achirona*. The presence of a particular inner marginal with few, flat, and blunt cusps in the latter could well justify a separate generic allocation. However, as the characterization of most of the species is still based on shell features, the use of radular characters for generic allocations is still difficult. Absalão and Pizzini (2002) discussed the artificial subgeneric arrangement in the subfamily Caecinae used by other authors. We agree that the knowledge of the relationships within the family is still very incomplete to warrant accurate allocations of species in subgenera or even in genera other than *Caecum*.

Judging by their recorded distributions, all three species reported here appear to be common in the shallow-water meiofauna along the Atlantic coast. The area of San Matías Gulf is part of the southern limits of the Argentine malacological province, according to different authors who agree considering the Peninsula Valdes area as its southernmost boundary.

Members of the family Caecidae have been recorded from Argentine waters. Some observations, as associated fauna or as prey, reported in ecological or marine biology papers, recognized caecids as part of food webs. However, no formal descriptions had been published so far. A possible reason could be the larger size of the traditional mesh used in marine surveys that render this type of gear ineffective to collect members of the family.

Arnaud and Poizat (1979) published some remarks on the ecology of three species of *Caecum* from the Mediterranean Sea. They showed that each species have different requirements of depth and habitat. In that sense, the hydrodynamic and the size of the sand grain play a crucial role in the distribution of species. They also mentioned the vertical migration of these species during two seasons: spring and summer with two different purposes, feeding and reproduction. Both species here described were collected during the Southern Hemisphere summer (in January). No egg capsules were found together with the adults; however, new collections in process particularly designed for this group could show their presence.

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Silvio F. B. Lima (Brazil) showed his new approach to the Caecidae and through the friendly discussion helped to clarify the identity of the material. Renata dos Santos Gomes (Brazil), Mauro Pizzini (Italy) and Robert Moolenbeek (The Netherlands) kindly sent publications and advice that really helped to finish this manuscript. Brenda Doti and Daniel Roccatagliata (Argentina) helped to collect and sort the samples. We acknowledge funding by the Consejo Nacional de Investigaciones

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LITERATURE CITED

- Absalão, R.S. 1994. A new species of the genus *Caecum* (Prosobranchia: Mesogastropoda) from Southern Brazil. *Journal of Conchology* 35: 137–140.
- Absalão, R.S. 1995. Ocorrência de *Caecum butoti* Jong & Coomans no Brasil (Rissoidea; Gastropoda; Mollusca). *Biociencias* 3 (1): 207–211.
- Absalão, R.S. 1997. *Caecum eliezerei* sp. nov. (Prosobranchia: Mesogastropoda): A new species from Brazil. *The Veliger* 40: 271–273.
- Absalão, R.S. and R.S. Gomes. 2001. The species usually reported in the subgenus *Brochina* (*Caecum*, Caecidae, Caenogastropoda) from Brazil and some relevant type specimens from western Atlantic. *Bolletino Malacologico* 37: 9–22.
- Absalão, R.S. and M. Pizzini. 2002. Critical analysis of subgeneric taxa of the Subfamily Caecinae (Caenogastropoda: Caecidae). *Archiv für Molluskenkunde* 131:167–183.
- Arnaud, P.M. and C. Poizat. 1979. Données écologiques sur des Caecidae (gastéropodes prosobranches) du Golfe de Marseille. *Malacologia* 18: 319–326.
- Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. *Zoologische Verhandlungen* 214: 1–188.
- Bandel, K. 1996. Phylogeny of the Caecidae (Caenogastropoda). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 79: 53–115.
- Carpenter, P.P. 1858. First steps towards a monograph of the Caecidae, a family of Rostriferous Gasteropoda. *Proceedings of the Zoological Society of London* 26: 413–444.
- Fleming, J. 1813. Mollusca. In: Brewster, D. (ed.) *The Edinburgh encyclopaedia*: conducted by David Brewster, with assistance of gentlemen eminent in science and literature. Vol. 7. Edinburgh.
- Farinati, E.A. 1994. Micromoluscos (Gastropoda y Bivalvia) del Holoeeno del área de Bahía Blanca, Argentina. *Ameghiniana* 31: 303–315.
- Folin, L. de 1868. Les Fonds de la Mer I, Baie de Bahia: 48–51; Rade de Rio de Janeiro: 51–54, pl. 5. Savy, Paris.
- Folin, L. de. 1868–9. Observations on the septum of the Caecidae; and some remarks on the subject of the suppression of the genera *Brochina* and *Strebloceras* or *Phleboboceras*. *Journal of the Linnean Society, Zoology* 10: 254–264. [According to the JLS, pages 197–260 were published on November 26, 1868 and 261–330 on January 8, 1869].
- Folin, L. de 1874. Sur les côtes du Brésil. *Les Fonds de la Mer* 2: 210–214, pls. 9–10. Savy, Paris.
- Folin, L. de 1877. Note relative au genre *Parastrophia*. *Journal de Conchyliologie* 25: 203–207.
- Di Geronimo, I., S. Privitera, and C. Valdovinos. 1995. *Fartulum magellanicum* (Prosobranchia, Caecidae): A new species from the Magellanic Province. *Boletín de la Sociedad de Biología de Concepción* 66: 113–118.
- Gomes, R.S. and R.S. Absalão. 1996. Lista comentada e ilustrada dos Caecidae (Mollusca, Prosobranchia, Mesogastropoda) da operação Oceanográfica Geomar XII. *Revista Brasileira de Zoologia* 13: 513–531.

- Gotze, E. 1938. Bau und Leben von *Caecum glabrum* (Montagu). Zoologisches Jahrbuch (Abteilung Systematik und Ökologie) 71: 1–190.
- Gray, J. E. 1850. Catalogue of the mollusca in the collection of the British Museum. Part II, Pteropoda. Newnan, London, 45 pp.
- Klappenbach, M. 1964. La familia Caecidae (Moll. Gastr.) en aguas uruguayas. Comunicaciones de la Sociedad Malacológica del Uruguay 1 (6): 145–149.
- Lange de Morretes, F. 1949. Ensaio de Catálogo dos moluscos do Brasil. Arquivos do Museu Paranaense 8: 1–216.
- Lange de Morretes, F. 1954. Dois novos moluscos do Brasil. Arquivos do Museu Paranaense 10: 331–336.
- Leal, J.H. 1991. Marine Prosobranch Gastropods from Oceanic Islands off Brazil. W. Backhuys, Oegstgeest, 418 pp.
- Lightfoot, J. 1992. Caecidae of the Western Atlantic part 2, conclusion. Of Sea and Shore 15: 23–31.
- Lima, S.F.B., F.N. Santos, and R.S. Absalão. 2013. New species of *Caecum* (Caenogastropoda: Rissoidae: Caecidae) from the Atlantic coast of South America (Brazil) with a description of the protoconch and growth stages. Zoological Science 30: 767–778.
- Marcus, E. and Marcus, Ev. D. B. -R. 1963. Mesogastropoden von der Küste São Paulos. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur Mainz 1963, 1: 5–105.
- Penchaszadeh, P. 1973. Comportamiento trófico de la estrella de mar *Astropecten brasiliensis*. Ecología 1: 45–54.
- Rehder, H.A. 1946. Additional notes on the dates of publication of Les Fonds de la Mer. Proceedings of the Malacological Society of London 27: 74–75.
- Rios, E.C. 1985. Seashells of Brazil. Editora da Fundação Universidade do Rio Grande, Rio Grande, 328 pp.
- Rios, E.C. 1994. Seashells of Brazil. Editora da Fundação Universidade do Rio Grande, Rio Grande, 368 pp.
- Rios, E. 2009. Compendium of Brazilian Sea Shells. Evangraf, Rio Grande, RS, 676 pp.
- Scarabino, F. 2004. Lista sistemática de los gastropoda marinos y estuarinos vivientes de Uruguay. Comunicaciones de la Sociedad Malacológica del Uruguay 8 (84–85/86–87): 305–346.
- Stuardo, J. 1962. *Caecum chilense*, nuevo molusco para Chile. Gayana, Zoología 5: 3–9.
- Stuardo, J. 1970. Sobre los representantes chilenos de la familia Caecidae (Mollusca: Gastropoda). Boletín de la Sociedad de Biología de Concepción 42: 183–190.
- Winckworth, R. 1941. Les Fonds de la Mer: Dates of Publication. Proceedings of the Malacological Society of London 24(4): 149–151.

A new melanopsid (Gastropoda) species from the middle Miocene Kupres Basin (Bosnia and Herzegovina)

Thomas A. Neubauer¹

Oleg Mandić

Mathias Harzhauser

Geological-Paleontological Department

Natural History Museum Vienna

1010 Vienna, Austria

thomas.neubauer@nhm-wien.ac.at

mathias.harzhauser@nhm-wien.ac.at

oleg.mandic@nhm-wien.ac.at

ABSTRACT

Melanopsis fateljensis (Caenogastropoda: Cerithiimorpha: Melanopsidae) is described as a new species from the early Middle Miocene lacustrine deposits of the Kupres Basin. Similarities to other co-occurring melanopsids are discussed. Its unique morphology, in particular the elongate, stepped spire with prominent spiral bulges, clearly distinguishes the new species from all other Melanopsidae known from the Neogene of Europe.

Additional Keywords: *Melanopsis*, freshwater gastropod, new species, Dinaride Lake System, Langhian

INTRODUCTION

Recently, Neubauer et al. (2013a) provided a taxonomic revision of the molluscan fauna of the Kupres Basin in Bosnia and Herzegovina, which was only poorly known by then (Brusina, 1902; Kochansky-Devidé and Slišković, 1981; Jurišić-Polšak and Slišković, 1988). The long-lived freshwater lake present in this basin during the early middle Miocene is part of the Dinaride Lake System, a collective of early to middle Miocene freshwater lakes in the Dinaride Mountain Chain (Figure 1; Krstić et al., 2003; Harzhauser and Mandić, 2008; De Leeuw et al., 2012; Mandić et al., 2012). The well-preserved fauna proved to be highly endemic, with two genera and five species newly described and 30% of the fauna endemic to Lake Kupres. Even well-studied coeval, nearby lakes, like Lake Sinj (Neubauer et al., 2011) and Lake Gacko (Neubauer et al., 2013b), showed only a low faunistic affinity, with a maximum of 38.9% of shared taxa. Another striking feature was the high percentage of sculptured morphologies, including

teleoconch microsculpture in one species, interpreted as a reaction to the oversaturation of calcium carbonate in the water under the existing alkaline, hard-water conditions (e.g., West et al., 1991).

Shortly after, another taxonomic work on the ostracod and gastropod fauna of the region around Kupres was published by Krstić et al. (2013). This study dealing with an outcrop located about 2 km ENE of Fatelj Hill revealed a different assemblage with species known from the Sinj, Drniš, and Gacko basins (Figure 1) and none of those described by Neubauer et al. (2013a). The fauna is characterized by few species of the genera *Gyraulus*, *Fossarulus*, *Bania*, and “*Pseudamnicola*” (both occurring species were recombined with *Bania* by Neubauer et al., 2013a). Such a faunal composition with pulmonate and typical pioneer species corresponds to those found in the Gacko and Sinj basins and points to rather stressed, ephemeral conditions at the basin margin in this particular stratigraphic level (Mandić et al., 2009; 2011; Neubauer et al., 2011; 2013b). These deposits were classified as “Ottangian” (middle Burdigalian) by Krstić et al. (2013), but should rather be placed in the early Langhian as discussed by Neubauer et al. (2013a).

The aim of the present study is to fix a misidentification of a melanopsid species by Neubauer et al. (2013a). Our taxonomic reinvestigation revealed clear differences to the species with which the taxon was previously identified in Neubauer et al. (2013a) and to all other melanopsids known from the European Neogene, urging the description of a new species.

MATERIALS AND METHODS

The material derives from an outcrop at the northwestern slope of a small hill, termed Fatelj, about 4 km SW of the town Kupres in Bosnia and Herzegovina (43°58'17.2" N, 17°14'06.9" E, 1140 m). The section is approximately 3 m thick and covers three lithological units briefly discussed

¹ Corresponding author

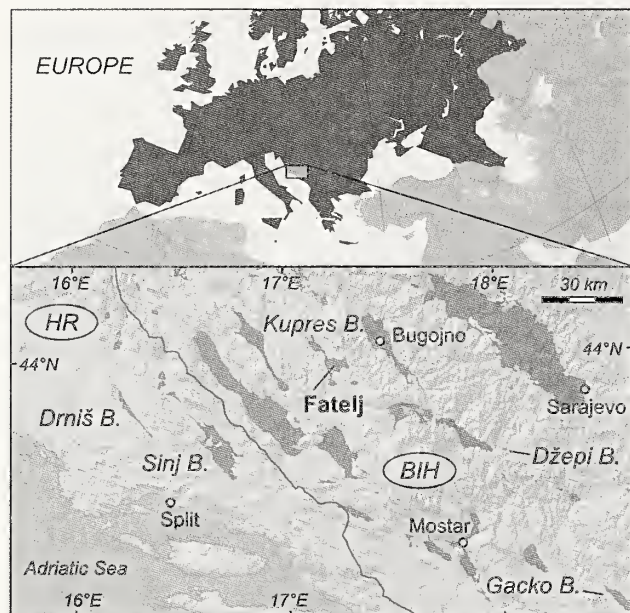


Figure 1. Geographical overview over the study area with indication of the main sedimentary basins harboring paleolakes mentioned in the text (modified after Neubauer et al., 2013a).

in Neubauer et al. (2013a). An age of the deposits of 15.5 ± 0.2 Ma (= early Langhian or early Badenian in terms of regional Paratethys stages) is suggested by the appearance of the dreissenid bivalve *Mytilopsis aletici* (Brusina, 1907), which is a good biostratigraphic marker due to the rapid evolution of these bivalves in the Dinaride Lake System (Kochansky-Devidé and Slišković, 1978, 1981; De Leeuw et al., 2010; Harzhauser and Mandić, 2010). Eleven samples were taken from units 1 and 3. Samples 090709/4 and 090709/5, containing the herein investigated species, were treated with diluted hydrogen peroxide and washed through two sieves with 2 mm and 0.5 mm mesh size. When necessary, specimens were cleaned from sediments with an ultrasonic device. The material is stored in the collection of the Natural History Museum of Vienna, Austria (NHMW 2011/0138).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1795
 Subclass Caenogastropoda Cox, 1960
 Order Cerithiimorpha Golikov and Starobogatov, 1975
 Superfamily Cerithioidea Fleming, 1822
 Family Melanopsidae H. Adams and A. Adams, 1854
 Subfamily Melanopsinae H. Adams and A. Adams, 1854

Genus *Melanopsis* Férussac, 1807

Melanopsis fateljensis new species (Figures 2–11)

Melanopsis sp.—Brusina, 1902: pl. 29, figs 23–26.

Melanopsis mojsisovicsi (Neumayr, 1880) comb. nov.—
 Neubauer et al., 2013a: 137, figs 5E–F, I–K (non
Melanoptychia Mojsisovicsi Neumayr, 1880).

Diagnosis: Shell conical, with elongate and distinctly stepped spire, with strong bulges below the sutures and a marked shoulder between whorl flank and base; aperture small, ovoid, with very small anterior canal.

Description: Shell high-conical, slender, elongate, with 7–10 whorls; proportions variable, with broader shells sometimes present. Protoconch bulbous, dome-shaped, highly convex; number of whorls unknown; initial part elevated, not covered by successive whorls; surface smooth. First few shell whorls form regularly conical outline; beginning about with fifth whorl, weak shoulder emerges near upper suture; shoulder increases in strength incrementally, eventually forming a broadly convex bulge. At transition of whorl flank to base, marked angle occurs, forming second, weaker bulge; weak and broad concavity is formed between both bulges, only visible on last 1–2 whorls. Upper bulge may have irregular course at upper suture in some specimens. Last whorl reaching 60–70 % of total height; base straight. Aperture small, slender-ovoid, with anterior and posterior tip forming acute, almost rectangular angles; callus weakly expressed, glossy; outer lip sharply terminated, not reflected; siphonal canal very short and narrow, not extended or reflected; fasciole narrow, very weak. Growth lines prosocylt to slightly sigmoidal (because of bulges), usually indistinct; occasionally and/or temporarily more prominent (Figures 9–10). Coloring very rarely preserved, consisting of thin, vertical to slightly sigmoidal, moderately-spaced, dark yellow to orange lines; occasionally they form widely-spaced zigzag-lines on earlier whorls (penultimate whorl upwards; see Figure 6).

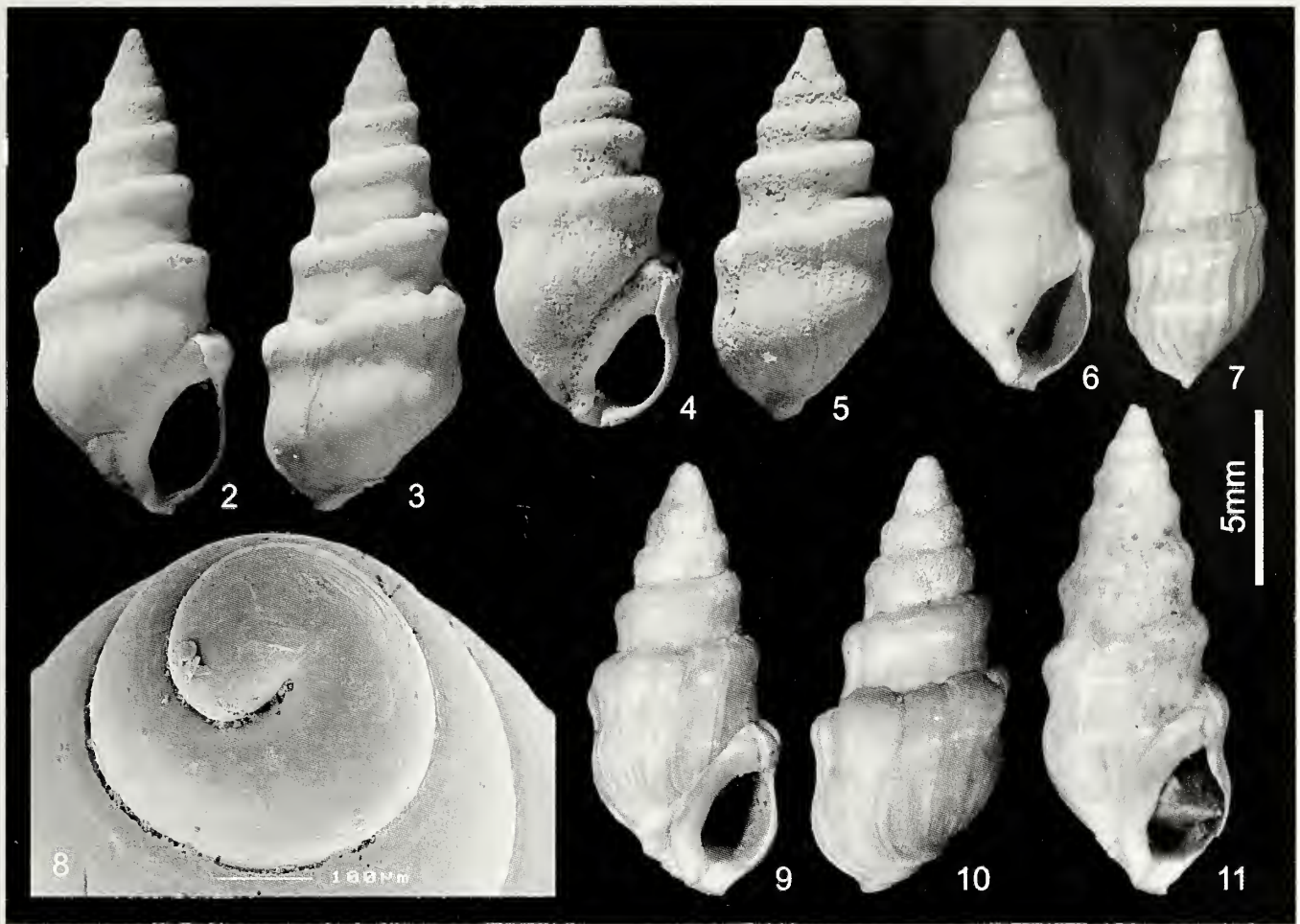
Type Material: Holotype (Figures 2–3), NHMW 2011/0138/0107a, 13.97 mm height \times 5.80 mm width; Paratype 1 (Figures 4–5), NHMW 2011/0138/0107b, 11.49 mm height \times 5.45 mm width; Paratype 2 (Figures 9–10), NHMW 2011/0138/0184, 12.41 mm length \times 5.61 mm width.

Additional Measurements: 10.47 mm height \times 4.74 mm width (Figure 6); 10.39 mm height \times 4.17 mm width (Figure 7); 14.10 mm height \times 5.47 mm width (Figure 11); 13.72 mm height \times 5.41 mm width; 15.01 mm height \times 5.67 mm width; 12.75 mm height \times 6.17 mm width.

Type Locality: NW slope of Fatelj hill near Kupres, —Bosnia and Herzegovina.

Stratum Typicum: Lower middle Miocene (= lower Langhian, lower Badenian).

Material Examined: Several hundred specimens from debris collection of Unit 3, 20 from sample 090709/4 and



Figures 2–11. *Melanopsis fateljensis* Neubauer new species, from the early middle Miocene of the Fatelj hill, Kupres Basin, Bosnia and Herzegovina. 2–3. Holotype (NHMW 2011/0138/0107a). 4–5. Paratype 1 (NHMW 2011/0138/0107b). 6. Specimen showing zigzag pattern on penultimate whorl (NHMW 2011/0138/0185). 7. Specimen with preserved coloration (NHMW 2011/0138/0186). 8. Protoconch view (NHMW 2011/0138/0107c). 9–10. Paratype 2 (NHMW 2011/0138/0184). 11. Elongate specimen (NHMW 2011/0138/0187). All illustrated specimens are from sample 090709/7 (debris collection of Unit 3).

a single specimen from sample 090709/5, all from the type locality.

Etymology: The new species is named after the type locality.

Geographic Distribution: So far only known from the Kupres Basin.

Taxonomic Remarks: This species is based on a misidentification by Neubauer et al. (2013a), whom erroneously identified the present material as *Melanopsis mojsisovicsi* (Neumayr, 1880) described from the roughly coeval locality Džepi (Bosnia and Herzegovina). A direct comparison is unfortunately impossible as the type material of *M. mojsisovicsi* has been lost. Other material available from Džepi and the descriptions and illustrations of Neumayr (1880) still show the differences quite clear. *M. mojsisovicsi* has a much higher last whorl and lacks the subsutural bulges so distinct for *M. fateljensis*. The columellar fold typical for *M. mojsisovicsi* is absent as

well. The two specimens illustrated in Brusina (1902: pl. 29, figs 23–26) as “*Melanopsis* sp.” correspond fully to the present species. *Melanopsis filifera* Neumayr, 1880 from the early middle Miocene deposits of Drvar (Bosnia and Herzegovina) also differs in a larger last whorl and a weakly to non-stepped spire. Aside from these we are not aware of any other melanopsid species similar to *M. fateljensis*.

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LITERATURE CITED

- Bandel, K. 2000. Speciation among the Melanopsidae (Caenogastropoda). Special emphasis to the Melanopsidae of the Pannonian Lake at Pontian time (Late Miocene) and the Pleistocene and Recent of Jordan. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 84: 131–208.
- Brusina, S. 1902. *Iconographia Molluscorum Fossilium in tellure tertiaria Hungariae, Croatiae, Slavoniae, Dalmatiae, Bosniae, Herzegovinae, Serbiae and Bulgariae inventorum*. Officina Soc. Typographicae, Agram, 30 plates.
- De Leeuw, A., O. Mandić, A. Vranjković, D. Pavelić, M. Harzhauser, W. Krijgsman, and K.F. Kuiper. 2010. Chronology and integrated stratigraphy of the Miocene Sinj Basin (Dinaride Lake System, Croatia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 155–167.
- De Leeuw, A., O. Mandić, W. Krijgsman, K. Kuiper, and H. Hrvatić. 2012. Paleomagnetic and geochronologic constraints on the geodynamic evolution of the Central Dinarides. *Tectonophysics* 530–531: 286–298.
- Harzhauser, M., T. Kowalke, and O. Mandić. 2002. Late Miocene (Pannonian) Gastropods of Lake Pannon with Special Emphasis on Early Ontogenetic Development. *Annalen des Naturhistorischen Museums in Wien* 103A: 75–141.
- Harzhauser, M. and O. Mandić. 2008. Neogene lake systems of Central and South-Eastern Europe: Faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 260: 417–434.
- Harzhauser, M. and O. Mandić. 2010. Neogene dreissenids in Central Europe: evolutionary shifts and diversity changes. In: Van der Velde, G., S. Rajagopal, and A. Bij de Vaate (eds.) *The Zebra Mussel in Europe*. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim, pp. 11–29.
- Jurišić-Poljak, Z. and T. Slišković. 1988. Slatkovodni gastropodi neogenskih naslaga jugozapadne Bosne. *Zbornik referata naučnog skupa "Minerali, stijene, izumrli i živi svijet BiH"*, Zemaljski Muzej Bosne i Hercegovine, Sarajevo, 7.-8. Oktobar 1988: 167–174.
- Kochansky-Devidé, V. and T. Slišković. 1978. Miocenske kongerije Hrvatske, Bosne i Hercegovine. *Palaeontologia jugoslavica* 19: 1–98.
- Kochansky-Devidé, V. and T. Slišković. 1981. Mlade miocenske kongerije Livanjskog, Duvanjskog i Kupreškog polja u jugozapadnoj Bosni i Hercegovini. *Palaeontologia jugoslavica* 25: 1–25.
- Krstić, N., L. Savić, G. Jovanović, and E. Bodor. 2003. Lower Miocene lakes of the Balkan Land. *Acta Geologica Hungarica* 46: 291–299.
- Krstić, N., G. Jovanović and L. Savić. 2013. Jezerski ostrakodi i prateći mekušci iz kupreškog polja, donji dio dinaridskog sistema jezera (Otnang) na visini od 1,150 m. *Zapisnici Srpskog Geološkog Društva* 2011: 1–25.
- Mandić, O., D. Pavelić, M. Harzhauser, J. Zupanić, D. Reischenbacher, R.F. Sachsenhofer, N. Tadej, and A. Vranjković. 2009. Depositional history of the Miocene Lake Sinj (Dinaride Lake System, Croatia): a long-lived hard-water lake in a pull-apart tectonic setting. *Journal of Paleolimnology* 41: 431–452.
- Mandić, O., A. De Leeuw, B. Vuković, W. Krijgsman, M. Harzhauser, and K.F. Kuiper. 2011. Palaeoenvironmental evolution of Lake Gacko (Southern Bosnia and Herzegovina): Impact of the Middle Miocene Climatic Optimum on the Dinaride Lake System. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299: 475–492.
- Mandić, O., A. De Leeuw, J. Bulić, K.F. Kuiper, W. Krijgsman, and Z. Jurišić-Poljak. 2012. Paleogeographic evolution of the Southern Pannonian Basin: 40Ar/39Ar age constraints on the Miocene continental series of northern Croatia. *International Journal of Earth Sciences* 101: 1033–1046.
- Neubauer, T.A., O. Mandić, and M. Harzhauser. 2011. Middle Miocene Freshwater Mollusks from Lake Sinj (Dinaride Lake System, SE Croatia; Langhian). *Archiv für Molluskenkunde* 140: 201–237.
- Neubauer, T.A., O. Mandić, M. Harzhauser, and H. Hrvatić. 2013a. A new Miocene lacustrine mollusc fauna of the Dinaride Lake System and its palaeobiogeographic, palaeoecologic, and taxonomic implications. *Palaeontology* 56: 129–156.
- Neubauer, T.A., O. Mandić, and M. Harzhauser. 2013b. The Middle Miocene freshwater mollusk fauna of Lake Gacko (SE Bosnia and Herzegovina): taxonomic revision and palaeoenvironmental analysis. *Fossil Record* 16(1): 77–96.
- Neumayr, M. 1880. V. Tertiäre Binnenmollusken aus Bosnien und der Hercegovina. *Jahrbuch der kaiserlichen und königlichen geologischen Reichsanstalt* 30(2): 463–486.
- West, K., A. Cohen and M. Baron. 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. *Evolution* 45: 589–607.

Attenuiconus marileeae, a new species of cone (Gastropoda: Conidae: Puncticulinae) from Curaçao

M.G. Harasewych

Department of Invertebrate Zoology
National Museum of Natural History
Smithsonian Institution
P.O. Box 37012
Washington, DC 20013-7012 USA
Harasewych@si.edu

ABSTRACT

Attenuiconus marileeae new species is described from deep reefs off southeastern Curaçao. It resembles *A. attenuatus*, *A. honkeri*, and *A. aureonimbosus* in size and general proportion of the shell, but is readily distinguished on the basis of its distinctive color pattern, which consists of a vivid orange-red base color with three bands of irregular, white flammules. *Attenuiconus marileeae* was collected at substantially greater depths than any of its Caribbean congeners. Only *A. aureonimbosus*, from the northeastern Gulf of Mexico, inhabits comparable depths. Like all species of *Attenuiconus*, nearly all specimens *A. marileeae* have one or more major repaired breaks indicative of unsuccessful attacks by crustaceans.

Additional Keywords: Deep Reef, Curasub, bottles, predation

INTRODUCTION

Over the past several years, sampling off southern Curaçao and adjacent islands using the manned submersible CURASUB as part of the Deep Reef Observation Project (DROP), a collaboration between the Smithsonian and Substation Curaçao, has greatly enriched our knowledge of the deep-reef faunas of the region and led to the discovery of range extensions and new species in multiple phyla.

Among the many mollusks collected is a new species of *Attenuiconus*, a genus of conids endemic to the tropical western Atlantic (Petuch, 2013; Tucker and Tenorio, 2013). Several specimens were among the hundreds of molluscan shells found in multiple glass bottles recovered from the ocean floor at depths ranging from 130–168 m. The age of the bottles ranged from mid-19th century to modern. Although nearly all these specimens were dead collected, they nevertheless provide insights into the molluscan biodiversity of the region, and include multiple range extensions and several new taxa. Many of the shells had at least one drill hole, and were likely brought into the bottles as food by small octopuses.

This new species is described and compared to *Attenuiconus attenuatus* (Reeve, 1844), the type species of *Attenuiconus*, a wide ranging species that occurs in southeastern Florida and throughout the Caribbean, including Curaçao, as well as to specimens of *Sandericonus sanderi* (Wils and Moolenbeek, 1979), the type species of *Sandericonus*, which was also present in the bottle samples.

SYSTEMATICS

Family Conidae Fleming, 1822

Subfamily Puncticulinae Tucker and Tenorio, 2009

Genus *Attenuiconus* Petuch, 2013

Attenuiconus Petuch, 2013: 212–213. Type species: *Conus attenuatus* Reeve, 1844, by original designation.

Diagnosis: “Shell small to average size for subfamily, very elongated, with straight sides and narrow, straight apertures; spires low or flattened, with projecting, mammillate protoconchs of 2 or 3 whorls; spire whorls may be flattened, or slightly canaliculated; shells generally smooth and polished, but some species have coarse sculpture of fine spiral threads; shells generally colored in yellows or oranges arranged in wide bands, but may be colored pink, salmon, reddish-orange with brown or white longitudinal flammules.” (Petuch, 2013: 212–213).

Remarks: In addition to the type species, which ranges from southern Florida throughout the Caribbean, Petuch (2013: 213) included within *Attenuiconus*: *A. eversoni* (Petuch, 1987) from Honduras, *A. honkeri* (Petuch, 1988) from Venezuela, *A. ignotus* (Cargile, 1998), from Honduras, Nicaragua and Colombia, as well as *A. poulosi* (Petuch, 1988) from Venezuela and Colombia. He noted that these species had previously been included in *Dauciconus* Cotton, 1945 by Tucker and Tenorio (2009), but that *Attenuiconus* may be distinguished from *Dauciconus* on the basis of its much

narrower and more elongate shell, and by its projecting protoconch. Tucker and Tenorio (2013) included *A. aureonimbosus* (Petuch, 1987), a species from the west coast of Florida, in *Attenuiconus*, but transferred *A. ignotus* to *Kellyconus* Petuch, 2013.

***Attenuiconus marileeeae* new species**
(Figures 12–18)

Description: Shell (Figures 12–16) of moderate size for genus (to 23 mm), with solid, narrow ($L/V \approx 2.1$), straight-sided, conical, low-conical spire, projecting protoconch, and narrow aperture. Protoconch (Figures 17–18) tall, conical, increasing in diameter from 291 μm to 850 μm in $3\frac{1}{4}$ evenly rounded, pitted glassy whorls. Protoconch forms a broad, smooth varix prior to transition to teleoconch (Figures 17, 18, arrows), marked by development of strongly tuberculate shoulder (17 tubercles on first teleoconch whorl, tubercles becoming weaker in subsequent whorls, absent by 5th whorl). Teleoconch with up to 8 sharply shouldered, straight-sided whorls. Suture adpressed in early whorls, may become shallowly impressed in later whorls. Sutural ramp narrow, weakly concave to flat, with 4–6 rounded cords between suture and shoulder. Last whorl smooth except for 5–6 broad, rounded spiral cords near anterior margin of shell. Aperture long, narrow ($L/V \approx 11$) with parallel sides, deflected from shell axis by $11\text{--}14^\circ$. Shell base color golden orange to orange red, with three bands of irregular white markings: one at and below the shoulder, one at mid-whorl, and one near the anterior margin of the shell. Band below shoulder broadest, consisting of very irregular, vaguely sigmoidal white flammules, which may be divided. White flammules extend over shoulder onto sutural ramp, but rarely reach suture. White blotches in relatively narrow band at mid-whorl range from small and compact (Figure 8) to large and amorphous (Figure 10), while flammules near anterior margin tend to form diffuse, oblique lines. Aperture color white. Radula, operculum, and periostracum unknown.

Type Material: Holotype, USNM 1195478. Paratypes 1–4, USNM 1240622, all from the type locality. Paratype 5, Petuch collection, also from the type locality.

Type Locality: Off the Sea Aquarium, Bapor Kibra, Willemstad, Curaçao, $12^\circ 04.48' \text{ N}$, $68^\circ 53.75' \text{ W}$, in glass bottles collected at 130–168 m, using the CURASUB submersible.

Distribution and Habitat: This new species is presently known only from off the southeastern coast of Curaçao, at depths of 130–168 m. Nearly all specimens have broken lips as well as one or more major repaired breaks, the latter indicative of prior, severe but unsuccessful attacks by crustaceans.

Etymology: This new species is named in honor of Marilee McNeilus in recognition of her longstanding interest in mollusks and her support of research. She participated in the submersible dives and assisted with

the specimen sorting that led to the discovery of this new species.

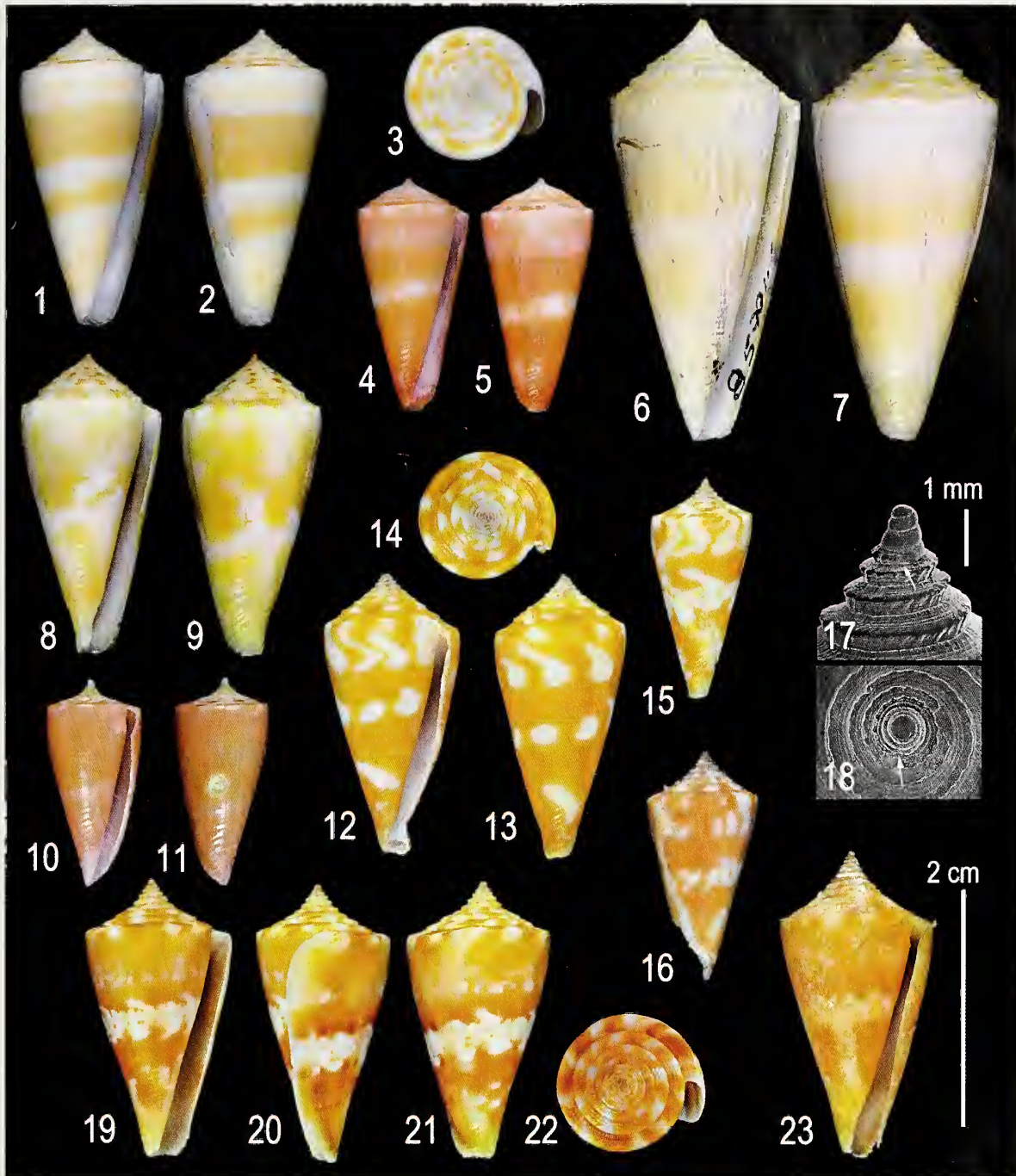
Comparative Remarks: *Attenuiconus marileeeae* resembles *A. attenuatus*, a wide-ranging species that occurs in southern Curaçao at shallower depths (Figures 1–3), in the size and proportions of the shell, but differs in having a more concave spire profile and more prominent spiral sculpture between the shoulder and suture. *Attenuiconus marileeeae* is most readily distinguished from all its congeners by its bright orange-red color and the large and distinctive patterns of white flammules that occur in three bands. The color patterns in *A. attenuatus* (Figures 1–5) and *A. honkeri* (Figures 6–7) usually take the form of fairly well-defined, parallel-sided bands of color. Both *A. eversoni* (Figures 10–11) and *A. poulosi* are easily distinguished from *A. marileeeae* by their flatter spires and more pointed early whorls, as well as by their more uniformly salmon-colored shells. *Attenuiconus aureonimbosus* (Figures 8–9) is similar to *A. marileeeae* in shell shape and proportion. It shares a similar pattern of irregular, nebulous white flammules, but is much paler in color. However, this species and *A. eversoni* tend to have a series of very fine spiral brown bands of spots, most evident between the shoulder and mid-whorl that are not present in *A. marileeeae*.

Attenuiconus marileeeae is easily separated from *Sandericonus sanderi*, a species of similar size and base color that also occurred among the specimens collected from the bottles. *Sandericonus sanderi* (Figures 14–18) has a broader shell with a flatter, more concave spire, a sharper shoulder, and a broad whitish band with nebulous margins at mid-whorl.

DISCUSSION

Conus, one of the original Linnean genera (Linnaeus, 1758), had, until recently, been considered to be the most species-rich modern marine genus, with more than 500 extant and several hundred extinct species (e.g., Röckel, Korn and Kohn, 1995; Duda, Kohn and Palumbi, 2001). Subsequent studies, which included information on radular morphology and molecular data, have partitioned the 743 cone species known at the time among three families, five subfamilies, and 114 living genera, an arrangement that is more in line with those of several other toxoglossan families (Tucker and Tenorio, 2013: 3). These authors note that the numbers are expected to increase, and the relationships among the taxa at all levels will continue to be refined as more data become available.

Within this new paradigm of conoidean systematics, *Attenuiconus* represents a small, poorly known genus limited to the western Atlantic, with greatest diversity in the southwestern Caribbean. The majority of species burrow in sandy bottoms at depths ranging from 10 to 50 m, although some of the SW Caribbean species and have been reported to live on sponge reefs (Petuch,



Figures 1–23. Species of *Attenuiconus* and *Sandericonus*. **1–5.** *Attenuiconus attenuatus* (Reeve, 1844), type species of *Attenuiconus* Petuch, 2013. **1.** Apertural, **2.** Dorsal, and **3.** Apical views of USNM 876325, off southeast shore of Curaçao, in 30–37 m, on sandy bottom. **4.** Apertural and **5.** Dorsal views of USNM 806476, off Dania, Florida, in 20 m, on sandy bottom. **6–7.** *Attenuiconus honkeri* (Petuch, 1988). **6.** Apertural, and **7.** Dorsal views of the holotype, USNM 859946, off the Los Monges Islands, Venezuela, in 35 m. **8–9.** *Attenuiconus aureonimbosus* (Petuch, 1987). **8.** Apertural, and **9.** Dorsal views of the holotype, USNM 859812, 50 km south of Apalachicola, FL, in 150 m. **10–11.** *Attenuiconus eversoni* (Petuch, 1987). **10.** Apertural and **11.** Dorsal views of the holotype, USNM 859878, off south coast of Utila Island, Bahia Islands, Honduras, among live *Agaricia* corals in 20 m. **12–18.** *Attenuiconus marileae* new species. **12.** Apertural, **13.** Dorsal and **14.** Apical views of the holotype, USNM 1195478. **15.** Dorsal view of Paratype 1. **16.** Dorsal view of Paratype 2. **17.** Lateral and **18.** Dorsal views of protoconch of Paratype 3. All type specimens from bottles collected in 130–168 m, using the CURASUB submersible, off the Sea Aquarium, Bapor Kibra, Willemstad, Curaçao. **19–23.** *Sandericonus sanderi* (Wils and Moolenbeek, 1979). **19.** Apertural, **20.** Lateral, **21.** Dorsal, and **22.** Apical views of USNM 1240614, Off Marie Pampoen, Willemstad, Curaçao, in 297 m, on sandy bottom. **23.** Apertural view of voucher specimen from the same locality that was the source of COI barcode sequence deposited in GenBank KJ751548. 2 cm scale bar applies to all shells, 1 mm scale bar applies to scanning electron micrographs of the protoconch. Arrows indicate transition from protoconch to teleoconch.

2013: 213). Only *A. aureonimbosus* from the northeastern Gulf of Mexico was reported from depths as great as 70–150 m. The depth at which *A. marileae* has been collected (130–168 m) is significantly greater than the bathymetric range for most *Attenuiconus*, but similar to that of *A. aureonimbosus*. As all available specimens of *A. marileae* were dead collected, it is possible that this species inhabits somewhat shallower waters, and that the shells may have rolled downslope and become occupied by hermit crabs prior to being brought into the bottles. However, other species of cones collected from the same bottles [(i.e., *Sandericonus sanderi* (Wils and Moolenbeek, 1979), *Conasprelloides villeginii* (P. Fischer and Bernardi, 1857), and *Dalliconus maei* (Deshayes, 1874)] are all known to inhabit the depths at which the bottles were collected (Rosenberg, 2009).

Living specimens of *Sandericonus sanderi* (Figures 19–23) were collected nearby, but at substantially greater depths (297 m).

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LITERATURE CITED

- Cargile, W.P. 1998. Description of *Conus ignotus*, a new species from Nicaragua. *Siratus* 2(14): 9–14.
- Deshayes, G.P. 1874. Description d'un cône nouveau des Antilles. *Journal de Conchyliologie* 22: 62–66.
- Duda, T.F. Jr., A.J. Kohn, and S.R. Palumbi, 2001. Origins of diverse feeding ecologies within *Conus*, a genus of venomous marine gastropods. *Biological Journal of the Linnean Society* 73: 391–409.
- Fischer, P. and A.C. Bernardi. 1857. Descriptions d'espèces nouvelles. *Journal de Conchyliologie* 5: 292–300, pl. 10.
- Linnaeus, C. 1758. *Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis ... Edicio decima reformata*. Impensis Direct. Laurentii Salvii. Holmae, Tom I. Animalia. [iv] + 823 pp.
- Petuch, E.J. 1987. New Caribbean molluscan faunas. Coastal Education and Research Foundation, Charlottesville, [v] + 154 + A1–A4, 29 pls.
- Petuch, E.J. 1988. Neogene history of tropical American mollusks. Coastal Education and Research Foundation, Charlottesville, [vi] + 217, 39 pls.
- Petuch, E.J. 2013. *Biogeography and Biodiversity of Western Atlantic Mollusks*. Boca Raton, Florida, CRC Press, xvii + 234 pp.
- Reeve, L. 1844. Monograph of the genus *Conus*. *Conchologica Iconica* 1:pls. 40–47.
- Röckel, D., W. Korn, and A.J. Kohn, 1995. *Manual of living Conidae*. Volume 1, Indo-Pacific Region. Christa Hemmen Verlag, Wiesbaden, 517 pp.
- Rosenberg, G. 2009. Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)] URL <http://www.malacolog.org/>
- Tucker, J.K. and M.J. Tenorio, 2009. Systematic classification of Recent and fossil conoidean gastropods. Hackenheim, Conchbooks, 296 pp.
- Tucker, J. K. and M. J. Tenorio, 2013. *Illustrated Catalog of the Living Cone Shells*. Wellington, FL, MdM Publishing, iv + 517 pp.
- Wils, E. and R. G. Moolenbeek, 1979. Two new *Conus* species from off Barbados, Lesser Antilles (Gastropoda, Conidae). *Bijdragen tot de Dierkunde* 49(2):255–260.

First American record of the exotic slug *Tandonia kusceri* (Gastropoda: Milacidae)

Jochen Gerber

Collections Center — Invertebrates
Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, IL 60605-2496 USA
jgerber@fieldmuseum.org

ABSTRACT

The terrestrial slug *Tandonia kusceri* (Pulmonata: Milacidae) is native to the Balkan Peninsula. This article reports the discovery of the species for the first time outside southeastern Europe, in Brookfield, Illinois, USA, a suburb of Chicago. Descriptions and photographs of live animals and reproductive organs are provided to facilitate the recognition of this potential pest species previously unrecorded from the Americas. *Tandonia kusceri* is compared with three other Milacidae species that have been introduced by humans into regions outside their native range, two of which have been recorded from North America. The known distribution and ecology of *T. kusceri* are summarized.

Additional Keywords: Introduced species, genital anatomy

INTRODUCTION

Terrestrial slugs have a long history of being introduced to the Americas from other continents. At least 26 species have been reported as having established populations in the USA and Canada (Turgeon et al., 1998; Reise et al., 2000, 2006; Grimm et al., 2009). Introduced slug species can pose threats to the environment, e.g., by competing with native species (Rollo, 1983), and they can become important agricultural pests (Mc Donnell et al., 2009 and references therein). Consequently, considerable amounts of manpower and money are spent by governments (e.g., U.S. Department of Agriculture [USDA]) to prevent additional species from entering North America, to limit the spread, and, if possible, eradicate limited occurrences of newly introduced species. Nevertheless, ever-increasing international trade has the unfortunate side effect that additional alien slug species (along with other mollusks and other animals and plants) continue to be introduced to America (Robinson, 1999; Robinson and Slapcinsky, 2005). Efforts to prevent new introductions and to limit the spread of alien species, as well as attempts to discover the avenues of their

introduction, are more likely to be successful if introduced species are documented as early as possible (Reise et al., 2000; 2006; Robinson and Slapcinsky, 2005).

In this article, the first American record of the alien slug *Tandonia kusceri* (H. Wagner, 1931) is reported. Photographs and descriptions of the animal and its genital anatomy are provided as identification tools.

MATERIALS AND METHODS

Voucher material has been deposited in the Mollusk Collection of the Field Museum of Natural History, Chicago (FMNH) and the USDA National Mollusk Collection, Philadelphia (USDA):

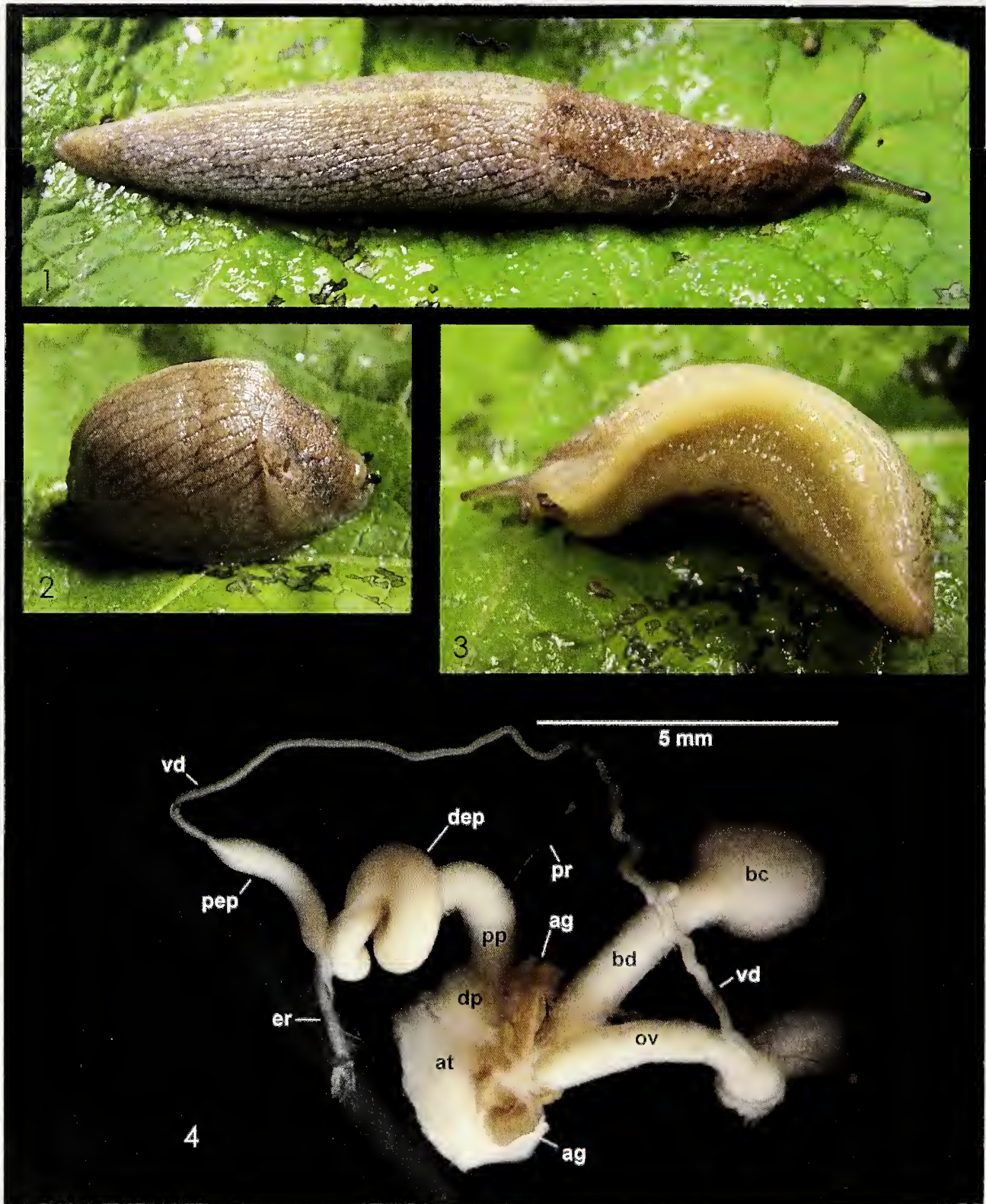
USA, Illinois, Cook County, Brookfield, near the intersection of Jefferson and Harrison Avenues, 41°49'42" N, 87°51'23" W, 190 m a.s.l., crawling on concrete porch after rain, at about 23:00h, 21 June 2013, leg. M.K. Thayer (FMNH 328572: 8 specimens preserved in 70% ethanol + tissue samples of 5 of these specimens in 95% ethanol; USDA 140056: 2 specimens preserved in 70% ethanol).

Same locality, but found in front yard, buried 10 cm deep in garden soil; 5 October 2013, leg. M.K. Thayer (FMNH 328573: 1 specimen in 70% ethanol; FMNH 328574: 1 dried specimen [mummified after escape from container in which specimens were kept]).

IDENTIFICATION

The descriptions (Figures 1–4) given here are based on the Brookfield specimens of *T. kusceri*.

External Morphology: Fully extended, mature specimens ca. 7 cm long, rather slender. Length of mantle shield in the front half of the body about 1/3 total body length. Breathing pore at about 3/4 of the mantle length from the anterior mantle margin, on the right side of the mantle shield. Mantle shield with a horseshoe-shaped groove open posteriorly. Surface of mantle shield granular. A keel extends along the middle of the dorsum,



Figures 1–4. *Tandonia kusceri* from Bolingbrook, Illinois, USA (FMNH 328572). 1. Extended specimen, length about 6.5 cm. 2. Contracted specimen. 3. Animal with sole exposed. 4. Distal portion of the reproductive tract. Abbreviations: **ag**, accessory gland; **at**, genital atrium; **bc**, bursa copulatrix; **bd**, duct of bursa copulatrix; **dep**, distal part of epiphallus; **dp**, distal part of penis; **er**, epiphallus retractor; **ov**, oviduct; **pep**, proximal part of epiphallus; **pp**, proximal part of penis; **pr**, penis retractor; **vd**, vas deferens.

from the tail end to the posterior edge of the mantle shield. Back and sides with about 15 diagonal rows of flattened tubercles on each side. When resting, specimens can contract strongly antero-posteriorly, so as to attain nearly a half-circle shape when seen from the side.

Overall color light yellowish- to pinkish-brown, becoming lighter toward the sole. Black pigment concentrated in the furrows separating the skin tubercles, which results in a reticulated pattern. Keel lighter-colored than back, without black pigment. Mantle diffusely speckled with dark pigment. A dark band present on either side along the branches of the horseshoe groove. Another, somewhat less distinct longitudinal pigment band in the center of the mantle shield. Head and tentacles brownish-grey. Sole tripartite, uniformly pale yellowish, without dark pigment. Mucus of body and sole colorless, transparent, slightly milky when animal irritated.

Genitalia: Ootestis in the dissected specimens ($n=2$) large, suggesting sexual maturity. Hermaphroditic duct long and thin. Albumen gland large (again, suggesting sexual maturity), elongated and bent. Spermiduct wide and twisted. Vas deferens thin and almost 1.5 times as long as penis and epiphallus combined, opening apically into the conically attenuated proximal end of the epiphallus. Epiphallus tubular, wider distally than proximally, very long, about five times as long as the penis, intensely coiled and twisted. A broad retractor muscle inserting on the epiphallus about $\frac{1}{4}$ of its length from its proximal end. Boundary between epiphallus and penis marked by the insertion of a thin second retractor muscle. Penis with two distinct sections: a tubular proximal part about as wide as the distal epiphallus or hardly wider, and a distal part that is short and globular, about twice as wide as the proximal part.

Oviduct tubular, straight or but lightly bent. Bursa copulatrix large, spherical. Bursa duct thick, its diameter slightly more than $\frac{1}{3}$ of the bursa diameter, and about twice as long as the bursa.

Accessory glands are two crinkled lobes, one roundish, the other elongated, that are attached to the vagina at the transition to the oviduct and bursa duct. The glands are of a beige color (as opposed to the white surrounding reproductive organs). Vagina and atrium short.

Epiphallus and bursa copulatrix with its duct were examined for the presence of a spermatophore but none was observed.

Distribution: The native distribution area of *T. kusceri* lies in the Balkans. It stretches from Central Serbia through FYR Macedonia, northeastern Greece, and Bulgaria to European Turkey and Southeast Romania (Dedov and Mitev, 2011; Reischütz, 1988; Wiktor, 1987; 2001). Occurrences of the species in Croatia, coastal Southwest Ukraine, and Crimea are presumed to be the result of human introductions (Son, 2010; Sysoev and Schileyko, 2009; Wiktor, 1987; 1996).

Ecology: According to Wiktor (1987), *T. kusceri* is a "species of very high ecological tolerance, occurring in biotopes of various humidity, most often found in places of large quantity of loose stones, under which it shelters. Occurring in shrubs, woods, stone debris, and synanthropically. Usually in large numbers, especially on limestone, and in biotopes heavily destroyed by man (wasteland, dumps, ruins)." Recorded elevations range from sea level (e.g., Varna, Bulgaria and Odessa, Ukraine; Wiktor, 1983; 1987; Son, 2010) to 1450 m a.s.l. (Osogovo Mountains, FYR Macedonia; Dedov and Mitev, 2011). Welter-Schultes (2012) states that *T. kusceri* occurs "in Bulgaria in up to 2000 m." However, none of the references he gives contains such an elevation record and it is unclear on what this statement is based.

According to observations at the Bolingbrook site, *T. kusceri* is only active at night. On 5 October 2013 two specimens were discovered during the day, buried 10 cm deep in garden soil. One of the specimens collected in October 2013 was held captive until late March 2014. The specimen was strictly nocturnal in its habits. During the day it stayed buried in the soil covering the bottom of the container rather than using items like pieces of tree bark that were offered for shelter.

DISCUSSION

Several species in the Milacidae, namely *Milax gagates* (Draparnaud, 1801), *Tandonia budapestensis* (Hazay, 1881) and *Tandonia sowerbyi* (A. Férussac, 1823), are known as invasives in areas far beyond their native southern European range. *Milax gagates* has been introduced around the world including North and South America (Wiktor, 1987; Turgeon et al., 1998; Grimm et al., 2009; McDonnell et al., 2009) and *T. budapestensis* has been recorded in the eastern United States (Reise et al., 2006). Consequently, it seemed likely that the milacids from Brookfield belonged to one of these tramp species. However, the attempt to assign the specimens to one of these species based on external characters failed. Dissections clearly showed that the Brookfield specimens were not conspecific with any of these invasives, but that they instead belonged to *Tandonia kusceri*, a species that had not been found previously outside of south-eastern Europe.

The combination of an extremely long vas deferens and epiphallus, the latter being intensely coiled and twisted, a short, bipartite penis, and a large, bulbous bursa with a thick tubular duct is unique among the Milacidae and allows for easy recognition of *T. kusceri*. Figure 4 shows the distal parts of the reproductive tract of a specimen from Bolingbrook (FMNH 328572). It resembles Wiktor's (1987: 258–259, fig. 155) description and drawing of the genital anatomy of *T. kusceri* very closely. The only differences are: Wiktor shows a constriction at the insertion of the penis retractor, i.e., at the epiphallus-penis boundary. No such constriction is discernible in the Bolingbrook specimen. Secondly, the

broad retractor inserting on the epiphallus about $\frac{1}{4}$ of its length from its proximal end is neither mentioned nor figured by Wiktor. However this feature is depicted in two of the drawings of the genitalia of *T. kusceri* (as *Milax* [M.] *kusceri*) by Grossu (1983: 223, fig. 139; 124, fig. 140).

Externally, the Bolingbrook specimens agree with the description of *T. kusceri* given by Wiktor (1987). Wiktor states that extended specimens are up to 10 cm long. The specimen figured by him (1987: 258, fig. 154) measures about 6.5 cm.

Other milacid species recorded from North America differ as follows (Wiktor, 1987):

Milax gagates – Vas deferens short; epiphallus club-shaped, proximally truncated, short; penis irregularly rounded, short, almost half the length of the epiphallus; bursa copulatrix elongated, its duct very short and indistinct; accessory glands open into the atrium (not the vagina) through numerous tubules (characteristic for genus *Milax*); atrial stimulator present (characteristic for genus *Milax*). Body tends to be uniformly dark grey or blackish, without pigment spots.

Tandonia budapestensis – Vas deferens short; epiphallus short, as long as or slightly longer than penis, cylindrical or club-shaped; penis irregularly rounded; bursa copulatrix oval to cylindrical, its duct thick and short. Body appearing variably blackish-brown due to dense black spotting on a dull cream or orange background; keel olive or orange, without black pigment. When resting, animals often curl into a c-shape, as opposed to other milacids which contract into a “hump” (Kerney and Cameron, 1979; Reise et al., 2006).

Tandonia sowerbyi has been introduced into large parts of southern and western Europe as well as South America and New Zealand, but has not been recorded from North America. It can be similar to *T. kusceri* in its external appearance (Wiktor, 2001) but differs clearly in its genital anatomy (Wiktor, 1987; 2001): Vas deferens long, narrow, twisted, about three times as long as the epiphallus (Wiktor, 1987: 301 states “twice as long” but fig. 215 on p. 302 shows the vas deferens to be clearly at least three times as long as the epiphallus); epiphallus a thick cylinder tapering and slightly bending toward the vas deferens; a strong retractor muscle inserting laterally on the epiphallus about $\frac{2}{3}$ of its length from its proximal end; two additional muscles, interpreted as retentors, inserting laterally (pointing away from each other) near the distal end of the epiphallus, close to a constriction marking the epiphallus-penis boundary; penis more or less cylindrical, about as wide as epiphallus, its length less than half to ca. $\frac{3}{4}$ of the epiphallus length; bursa copulatrix strongly elongated, tubular in younger specimens, distally wider and clearly delimited from duct in older specimens; bursa duct narrower and shorter than bursa.

At this point it is not clear if the *T. kusceri* population in Brookfield is the result of a recent introduction and restricted to the immediate area around the collection site, or if the species has been there for a number of years and occupies a wider area. We do not know how this exotic species was introduced. The fact that the discoverer, Dr. Margaret K. Thayer, who has lived at this address for the last 25 years and who, as an experienced zoologist, is trained to take notice of unusual animal occurrences, does not remember seeing this slug in previous years seems to point to a recent arrival on the Thayer property. However, it is currently impossible to state with certainty whether the slugs have recently migrated from nearby yards and gardens where they may have dwelled for some time and how and when they arrived there. I intend to monitor the *Tandonia* population in Bolingbrook and learn more about the extent of the infestation in the coming months.

The apparently very wide ecological amplitude of *T. kusceri* and its synanthropic tendencies (Wiktor, 1987) suggest that the species could be successful in becoming established in North America.

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LITERATURE CITED

- Dedov, I.K. and T. Mitev. 2011. Mollusks fauna (Mollusca: Gastropoda: Bivalvia) of Mountain Osogovo. *Acta Zoologica Bulgarica* 63: 37–46.
- Grimm, F.W., R.G. Forsyth, F.W. Schueler, and A. Karstad. 2009. Identifying land snails and slugs in Canada. Introduced species and native genera. Canadian Food Inspection Agency, Ottawa, iv + 168 pp.
- Grossu, A.V. 1983. *Gastropoda Romaniae*. 4. Ordo Stylommatophora. Suprafam.: Arionacea, Zonitacea, Ariophantacea și Helicacea. Editura Litera, București, 564 pp.
- Kerney, M.P. and R.A.D. Cameron. 1979. A field guide to the land snails of Britain and North-West Europe. Collins, London, 288 pp., 24 pls.
- Mc Donnell, R.J., T.D. Paine, and M.J. Gormally. 2009. Slugs: A Guide to the invasive and native fauna of California. University of California Agricultural and Natural Resources Publications 8336: 1–21.
- Reischütz, P.L. 1988. Beiträge zur Molluskenfauna Thrakiens und Ostmakedoniens, II. *Annalen des Naturhistorischen Museums in Wien, Serie B* 90: 341–356, pls. 1–2.
- Reise, H., J.M.C. Hutchinson, R.G. Forsyth, and T. Forsyth. 2000. The ecology and spread of the terrestrial slug *Boettgerilla pallens* in Europe with reference to its recent discovery in North America. *The Veliger* 43: 313–318.
- Reise, H., J.M.C. Hutchinson, and D.G. Robinson. 2006. Two introduced pest slugs: *Tandonia budapestensis* new to the

- Americas, and *Deroceras panormitanum* new to the Eastern USA. *The Veliger* 48: 110–115.
- Robinson, D.G. 1999. Alien invasions: The effects of the global economy on non-marine gastropod introductions into the United States. *Malacologia* 41: 413–438.
- Robinson, D.G. and J. Slapcinsky. 2005. Recent introductions of alien land snails into North America. *American Malacological Bulletin* 20: 89–93.
- Rollo, C.D. 1983. Consequences of competition on the reproduction and mortality of three species of terrestrial slugs. *Researches on Population Ecology* 25: 20–43.
- Son, M.O. 2010. Alien mollusks within the territory of Ukraine: sources and directions of invasions. *Russian Journal of Biological Invasions* 1: 37–44.
- Sysoev, A. and A. Schileyko. 2009. Land snails and slugs of Russia and adjacent countries. Pensoft Publishers, Sofia, 312 pp., 142 pls.
- Turgeon, D.D., J.F. Quinn, Jr., A.E. Bogan, E.V. Coan, F.G. Hochberg, W.G. Lyons, P.M. Mikkelsen, R.J. Neves, C.F.E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F.G. Thompson, M. Vecchiarelli, and J.D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, 2nd Edition. American Fisheries Society, Special Publication 26, Bethesda, ix + 526 pp.
- Welter-Schultes, F.W. 2012. European non-marine mollusks, a guide for species identification. Planet Poster Editions, Göttingen, pp. A1–A3, 1–679, Q1–Q78.
- Wiktor, A. 1983. The slugs of Bulgaria (Arionidae, Milacidae, Limacidae, Agriolimnidae — Gastropoda, Stylommatophora). *Annales Zoologici* 37: 71–206.
- Wiktor, A. 1987. Milacidae (Gastropoda, Pulmonata)—systematic monograph. *Annales Zoologici* 41: 153–319.
- Wiktor, A. 1996. The slugs of the former Yugoslavia (Gastropoda terrestrial nuda — Arionidae, Milacidae, Limacidae, Agriolimnidae). *Annales Zoologici* 46: 1–110.
- Wiktor, A. 2001. The slugs of Greece (Arionidae, Milacidae, Limacidae, Agriolimnidae — Gastropoda, Stylommatophora). *Fauna Graeciae* 8. Natural History Museum of Crete / Hellenic Zoological Society, Irakleio, VIII + 241 pp.

Erratum

In the last issue (Amano et al. 2014), on page 14, left-hand column, line 7, please replace “~*Adulomya*” for “?Adulomya”.

LITERATURE CITED

Amano, K., R.G. Jenkins, M. Ohara, and S. Kiel. 2014. Miocene vesicomyid species (Bivalvia) from Wakayama in southern Honshu, Japan. *The Nautilus* 128: 9–17.

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